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Growth and Survival of the Oak Wilt Fungus in Oak Blocks
Arthur D. Partridge **306**

Colchicine-Induced Polyploidy in *Abies*
Francois Mergen, Donald T. Lester **314**

Soil-Site Studies in Piedmont Hardwood and Pine-Hardwood Upland Forests
Lino Della-Bianca, David F. Olson, Jr. **320**

Foliar Absorption and Translocation of Phosphorus by Loblolly Pine Seedlings
C. S. Schopmeyer **330**

An Index for Comparing Equations Used in Constructing Volume Tables
George M. Furnival **337**

The Effect of Photoperiod on Growth, Photosynthesis, and Respiration of Loblolly Pine Seedlings from Two Geographic Sources
Wm. H. Davis McGregor, Robert M. Allen, Paul J. Kramer **342**

Field Identification of Roots of Conifers in the Inland Empire
R. L. Gilbertson, C. D. Leaphart, F. D. Johnson **352**

Shoot Elongation Characteristics of Forest Trees
Theodore T. Kozlowski, Richard C. Ward **357**

Dry-Matter Content of Loblolly Pine Needles Appears Unrelated to Geographic Seed Source
B. F. McLemore, A. B. Crow, P. C. Wakeley **373**

Influence of Cycloheximide on Growth of Mycorrhizal Fungi and on Mycorrhizae of Pine
Edward Hacskaylo **376**

Antibiotics for Control of Blister Rust on Western White Pine
Virgil D. Moss **380**

NOTES: New data on distribution of some true firs of the Pacific coast 349; Liquid dispersion method for mounting wood fibers on slides 369

REVIEWS: An annotated bibliography on the uses of statistics in ecology—a search of 31 periodicals 319; Principles of plant breeding 336; Forest entomology 351; Illustrated genera of wood decay fungi 368; The natural regeneration of *Eucalyptus regnans* 370; Minnesota lands 372; Timber utilization in Malaya 379

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Growth and Survival of the Oak Wilt Fungus in Oak Blocks

BY
ARTHUR D. PARTRIDGE

THE POSSIBILITY that oak wilt fungus (*Ceratocystis fagacearum* (Bretz) Hunt) is harbored and carried in oak wood products has led to restrictions on imports of American oak products into several countries (U.S. Forest Service 1958; U.S. Department of Agriculture 1958). There is, in fact, some justification for these restrictions. In the first place the fungus has been isolated from naturally invaded wood as long as 44 weeks after cutting (Englerth *et al.* 1956; Merek and Fergus 1954), and is known to persist in red oak (*Quercus rubra* L.) stumps as long as 2 years after infection (Young 1949). It will survive in the roots of oaks for as long as 3 years (Yount 1955). Moreover, the fungus has been successfully isolated at a depth of 1¼ inches in wilt-killed trees of the red oak group (Jones and Bretz 1955).

FIGURE 1. *Example of the technique employed to secure growth of the oak wilt fungus in oak wood blocks. The fungus has covered most of the outer surface of the sapwood after 10 days' incubation.*

However, in order to evaluate oak wood as a potential carrier of oak wilt and eventually to find methods for disinfecting oak wood products, more basic information on the mode and extent of wood penetration by the fungus is needed. A recent study was conducted at the Central States Forest Experiment Station to provide such information.

The study involved the effect of time and moisture on the invasion and survival of the oak wilt fungus in blocks consisting of both heartwood and sapwood and in blocks containing heartwood only. Histological studies were carried on in conjunction with both of these tests. Results of this study are presented here.

General Procedures

The methods described in this section apply to all of the tests in the following study and were derived from the results of preliminary investigations.

Test blocks approximately 1.5 x 1.5 x 2.0 inches in size were cut from sound, freshly severed, living white oak (*Quercus alba* L.) and black oak (*Q. velutina* Lam.) trees. Immediately after cutting, the blocks were sterilized by holding them for 6 days in

This work was done when the author was on the staff of the Central States Forest Expt. Sta., Forest Service, U. S. Dept. of Agric. He is now Assistant Professor of Forest Pathology, University of Idaho, Moscow, Idaho. Manuscript received March 20, 1961.

airtight containers to which 3 ml of propylene oxide was added for each 1,000 ml of container volume.

Half-pint jars with metal lids were used as containers for cultures and blocks. To provide sterile aeration, with little loss of moisture, four ¼-inch holes were drilled in the lids and plugged with cotton. Unbuffered vegetable-juice agar (selected as the best of a half-dozen media given preliminary tests) with a pH of about 4.5 was placed in each jar and the unit steam sterilized. The cultures were started by hypodermically injecting an endoconidial suspension through the cotton plugs. They were then incubated at 24° C ±3° C for approximately 10 days before being used to contaminate wood blocks.

After the blocks were sterilized, they were placed on cross-sectional end on the surfaces of the previously described cultures and incubated. After 14 days, the blocks were thoroughly invaded (Fig. 1); that is, the fungus could be isolated from sample points throughout the sapwood, although not necessarily from every chip, as preliminary tests had shown. The blocks were then removed from the cultures and placed in clean, sterile jars for the tests. Within these jars, humidity was high and wood dried very slowly. Longevity was considered in terms of elapsed time from this point.

The presence of the fungus in specific parts of each block was determined by splitting the block radially and culturing wood chips obtained from the freshly exposed surfaces. Care was exercised to insure that the fungus was not transferred from one part of a block to another on the instruments used during this procedure. Twenty-four chips were aseptically cut from the sapwood and heartwood portions of each block: Eight were cut parallel to the grain in the sapwood, eight were cut parallel to the grain in the heartwood, and eight were cut across the grain in both sapwood and heartwood (Fig. 2). Each chip was transferred to a water-agar plate and incubated for 14 days, after which time the presence or absence of the fungus was macroscopically noted.

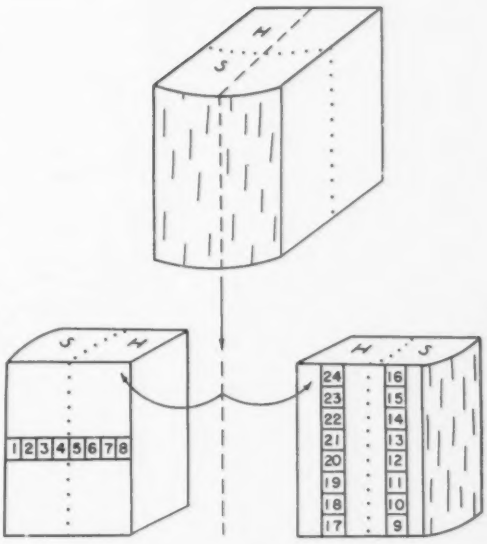

FIGURE 2. *Diagram illustrating the method of block sampling used in the tests. Above, a whole block; below, the split block. The dashed line indicates the splitting plane, and the curved arrows the relations of the resulting sections. S and H represent sapwood and heartwood, and the dotted line indicates the interface of these tissues. The checked area is the outer tangential face of the sapwood. Each numeral indicates the position of a single sample-chip.*

Tests in Blocks Containing Both Sapwood and Heartwood

Procedures. The effects of time and wood moisture on the penetration and survival of the fungus in wood were studied by artificially colonizing 204 blocks of white oak and 205 blocks of black oak. Each block contained approximately equal portions of sapwood and heartwood. The outer face of the sapwood was intact.

In one group of blocks moisture content was maintained at approximately 35 percent oven-dry weight. This was achieved by periodically determining the moisture content of an identical group of control blocks and aseptically adding water to the test blocks in proportion to that indicated as lost by the controls. The test blocks were

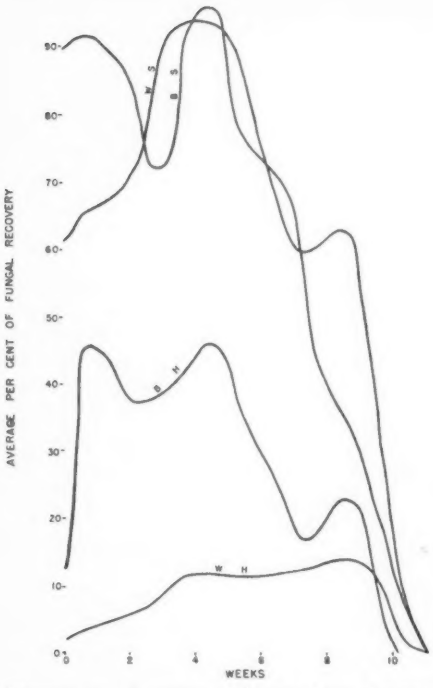

FIGURE 3. *Recovery of fungus from the sapwood and heartwood tissues of two species of oak wood when the wood moisture was not controlled (W, white oak; B, black oak; S, sapwood; H, heartwood). Initially the fungus was well distributed in these blocks.*

sampled for presence of the oak wilt fungus over a period of 12 to 15 weeks at 3 to 5 week intervals. In another group, wood moisture was not controlled and the blocks were permitted to dry in jars at room temperature. These blocks had an initial moisture content of approximately 47 percent and were sampled at 1-week intervals for 13 weeks. All samplings of both groups included a minimum of 10 contaminated blocks of each species for each time interval. The presence or absence of the fungus was recorded for each of the 12 sapwood and 12 heartwood chips from each block.

Results. Fourteen days' exposure of the blocks to cultures of the fungus resulted in an extensive invasion of the sapwood of both species. Invasion of heartwood was less frequent and less complete than that of the sapwood (Fig. 3).

A difference in recoveries, statistically significant at the 1 percent level, was found between the two oak species. Preliminary tests indicated no significant differences in recovery of the fungus due to variation in culture media, wood source, different dates of sampling and chipping, or fluctuations in incubation temperatures between 21° and 27° C. More recovery was obtained from black oak than from white oak; however,

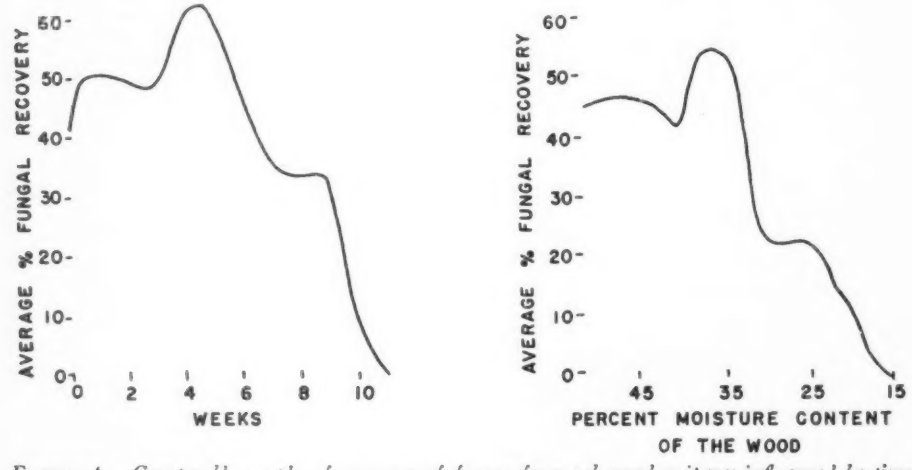

FIGURE 4. *Comparable graphs of recovery of fungus from oak wood as it was influenced by time and wood moisture.*

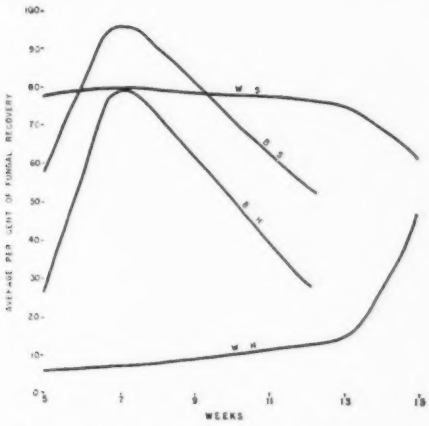

FIGURE 5. *The influence of time on recovery of fungus when wood moisture was relatively constant at the 35 ± 4 percent level (W, white oak; B, black oak; S, sapwood; H, heartwood).*

this was apparently due in part to the lesser recovery in white oak heartwood as compared to black oak heartwood, and is more accurately described by graphical analysis (Fig. 3).

The recovery rates from the sapwood and heartwood of both species fluctuated with time even though the fungus was well distributed in the blocks by the end of the initial 14-day exposure period. These fluctuations occurred at approximately the same times, although they were not of the same magnitude, in all tissues of both species. They corretspond to those obtained when recovery was related to wood moisture (Fig. 4)..

When wood moisture was maintained at a level of 30–35 percent, the longevity of the fungus in wood was increased (compare Figs. 3 and 5). Under test conditions, the fungus was recovered for as long as 12 weeks from black oak blocks, and as long as 15 weeks from white oak blocks. At the end of this test, the fungus was still recovered frequently, indicating an even longer potential for survival.

There was some indication that things other than wood moisture affected fungal recovery (Fig.5). Chief among these apparently was the effect of unexplained factors associated with progressing time, which in general resulted in decreasing recoveries. When wood moisture was held constant, the recovery rates in black oak increased at first and then decreased. In white oak, however, recoveries from the sapwood were initially high. They declined slowly and made a moderately sharp dip at about the 13th week. In the heartwood of white oak, the recovery rates were low at first. They increased slowly until the 13th week and then suddenly increased sharply. This is not greatly different from the increasing recovery in this tissue indicated in Figure 3, except for the sudden upswing at the end of the test. It should also be noted that this increase in recovery from white oak heartwood corresponded to the decline in recovery from the sapwood.

When all recoveries were plotted against wood moisture, a minimum and an optimum wood-moisture content for fungus recovery was indicated (Fig. 6). The optimum was about 35 to 40 percent (Figs. 4 and 6). The effects of wood-moisture contents above 50 percent on recovery and growth were probably not adequately tested

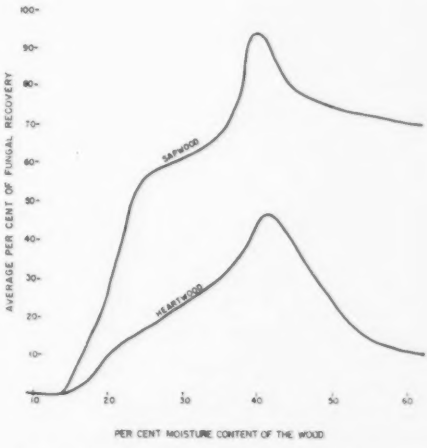

FIGURE 6. *Wood moisture as related to recovery of fungus based on data from all of the tests.*

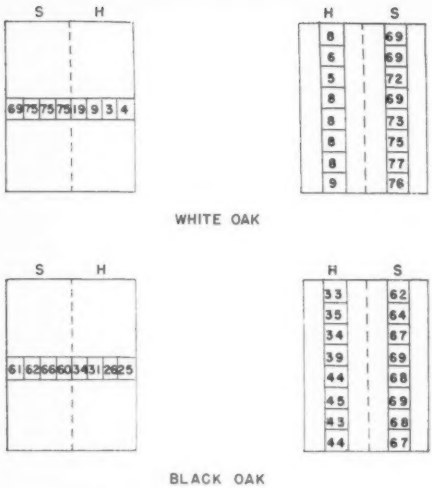

FIGURE 7. *Average recovery of fungus from each chipping position in the test blocks (compare with Fig. 2). The recovery is expressed as a numerical average for each position. H represents heartwood, S represents sapwood, dotted line indicates the interface of these tissues.*

here, since moisture contents of this magnitude were rare, and rapid surface drying in such wood distorted recovery rates. The minimum moisture content was 15 to 20 percent. Actually, there were very few recoveries from test blocks with less than 20 percent moisture. One of 205 black oak blocks contained the viable fungus at a moisture content of 16 percent, and two of 204 white oak blocks contained the viable fungus at moisture contents of 15 and 18 percent.

In some instances, even though certain blocks had moisture contents higher than 20 percent, the fungus was not recovered. This occurred in 19 percent of the white oak blocks and in 25 percent of the black oak blocks. These figures are somewhat misleading, however, because they represent all blocks and all time intervals. In reality, nonrecovery of the fungus occurred more often as time progressed. When the moisture content of wood became low enough to limit fungus survival, later increases in moisture in no case caused the fungus to revive.

In the sapwood of both species, the recovery rates for each chipping position were essentially the same (Fig. 7). In the heartwood, however, the fungus was recovered most frequently from the area adjacent to the sapwood, although there was also slightly greater recovery from the lower positions in the blocks.

The fungus was recovered from the heartwood of 35 percent of all blocks and from the sapwood of 77 percent of the blocks. In many instances, the fungus could be recovered from only a small portion of the available heartwood in a block, but could be recovered from most or all parts of the available sapwood. Recovery from black oak heartwood was generally greater than from white oak (Figs. 3, 5, and 7), but Figure 5 suggests that this situation may reverse with passing time.

Tests in Blocks of Heartwood

Procedures. These tests were designed to determine whether or not the fungus could penetrate into and survive in heartwood alone. Forty-five blocks of white oak and 45 of black oak heartwood were used. The blocks were contaminated and handled as previously described except that a thin layer of sapwood, which was present on these blocks during the period of fungal ingress, was removed at the beginning of the tests. All subsequent growth and survival of the fungus then occurred in isolated heartwood. In these tests, the sampling was done at approximately 2-week intervals for 10 weeks.

Results. These tests demonstrate that the fungus is capable of invading and surviving in oak heartwood. The organism was recovered from isolated black oak heartwood for 4 weeks and for 6 weeks in white oak blocks. Some recovery was realized from 13 percent of all blocks used in these tests. The depth of penetration, however, was generally far less than in sapwood. No relation between the moisture contents of these blocks and recovery therefrom could be found.

Histological Studies

Procedures. During the progress of the previously described tests, samples of the contaminated wood were examined microscopically and macroscopically. Some sections were cut by hand; others were cut on a microtome from embedded material. Stains were applied to some sections; other sections were unstained. This variety of procedures allowed observations of the material in a natural state and in a thin-sectioned or stained state. Standard histological procedures and stains were used where applicable.

Results. The histological studies of test blocks confirmed the presence of the organism in both sapwood and heartwood. Microscopic examination of sections from both species showed that the principal avenue of invasion was the wood rays. Indirect evidence of such penetration was also provided by macroscopic observations. The fungus, in growing on the blocks, rapidly covered the surfaces of the sapwood with a mycelial mass. In most cases, this growth originated at the terminals of wood rays, or at the cut ends of wood rays. When the blocks were flamed and placed in empty, sterile jars, the first new growth also developed from the rays. Microscopical studies of invaded wood indicated that penetration of the wood rays was intracellular and intercellular via natural interstices. Pit-pairs and intercellular spaces provided such avenues of advance, but there was no evidence of cell-wall dissolutions or of direct penetrations of cell walls.

Although the mycelium of the fungus was relatively abundant in the vessels of test blocks, and although sporulation was common on their exposed surfaces, no sporulation was observed in 500 sections taken from 20 different blocks of both species. It was first suspected that spores or sporophores might be present, but were lost during the histological procedures. Examination of numerous untreated hand sections from fresh blocks did not confirm this suspicion, and no spores could be removed from the blocks using a partial vacuum. Observations of whole blocks and block segments under either a dissecting microscope (10×–80×) or an incident-light microscope (100×–750×) also failed to reveal any sporulation occurring in the wood. In white oak the numerous tyloses, in all vessels except those of the outer annual ring, made the mycelium difficult to identify, although it was found occasionally.

Discussion

The tests show that the oak wilt fungus can invade and survive in the wood from white oaks or black oaks. Although this capacity has been reported previously (Englerth *et al.* 1956, Jones and Bretz 1955, Merek and Fergus 1954, Spilker 1953, Spilker and Young 1955), no invasions of heartwood have been mentioned. In these tests, it was found that the fungus could invade and survive in heartwood, although generally the sapwood was more quickly, frequently, and thoroughly invaded. In isolated heartwood, the fungus is capable of surviving for at least 4 weeks, while in the sapwood it is capable of surviving for at least 12 weeks. These observations indicate that oak heartwood is a less favorable substrate for the fungus than oak sapwood, which may explain why the fungus has not been recovered from the heartwood under natural conditions.

It has been reported that growth of the fungus in red oak wood appears to take place in the vessel lumina and intra-cellularly in the xylem parenchyma, with some hyphae penetrating the xylem parenchyma via the pits (Fergus and Wharton 1957). Radial growth through the pits of ray cells from the vessels of northern pin oak has also been reported (Struckmeyer and Kuntz 1954). Histological studies of contaminated black oak wood confirmed these former observations, but in white oak, except in the outer annual ring, mycelium was rarely observed in the vessels even though culturing showed the fungus to be present. Further study indicated that the principal avenues of invasion were the wood rays. Surface growths of the fungus from wood also implied that the fungus grew principally in

the rays. This mode of penetration would explain why white oak, with its occluded vessels, was invaded equally as fast as was black oak, with its open vessels. It might also explain the higher rates of recovery that were realized in the heartwood adjoining the heartwood-sapwood interface.

Mechanical penetrations or cell-wall dissolutions by the fungus were not noted. Fergus and Wharton (1957) also found this to be true; Brandt (1953), and Young and Brandt (1953) have shown that this organism fails to weaken oak wood under conditions which permit associated fungi to decrease the static-bending strength or tensile strength of that wood. From these facts, it can be concluded that the oak wilt fungus causes no known damage in invaded wood. In addition, no sporulation of the fungus in dead oak wood was indicated by any of several methods. Fergus and Wharton (1957) also found no endoconidia in more than 300 sections of invaded red oak stems and roots.

In these tests, the fungus was seldom isolated when the wood moisture was less than 20 percent, indicating that moisture is critical for the survival of the fungus in oak wood. This finding closely parallels those reported by Englerth *et al.* (1956), and Spilker and Young (1955). The graphical analyses of the data show comparable fluctuations in recovery of the fungus as influenced by time or by wood moisture (Figs. 3 and 4), which imply that the fungus is extremely sensitive to wood-moisture variations. This was further corroborated by the increased longevity resulting when wood moisture was maintained at a relatively high level.

Maximum recovery ot the fungus was obtained from wood with a 35-40 percent moisture content. Certain other factors (i.e., possibly autotoxin formation, or substrate exhaustion, etc.), associated with the passage of time, also may have exerted an influence. Spilker and Young (1955) reported that, in black oak, there appears to be a decrease in the viability of *C. fagacearum* with the passing of time. The general trend toward less survival in moisture-controlled blocks as time progressed (Fig. 5) and the decreasing rate of recovery with passing time at moisture contents greater than 20 percent are indications of this phenomenon. However, these time-associated factors appeared to be less critical in governing the recovery of this fungus from wood than was the moisture content of the wood.

Relatively long potential periods of survival and the ramified, relatively deep penetration of the fungus will necessitate unusual procedures to disinfect wood products. Surface treatments, including superficial heating, will not assure that the organism is killed. Increased temperature, longer exposures, or other methods should be employed, especially with timbers, veneer bolts, or the like. Sterilization with suitable fumigants under controlled conditions is now being investigated.

Summary

In laboratory tests small blocks of oak wood were artificially contaminated with the oak wilt fungus (*Ceratocystis fagacearum* (Bretz) Hunt). The fungus lived in these blocks for as long as 15 weeks. Extensive invasion of oak sapwood was common, and some invasion of oak heartwood was recorded. The fungus survived in isolated heartwood for as long as 6 weeks. Wood moisture was important in determining the longevity of this organism. Few isolations were successful when wood moisture was less than 20 percent. Maximum recovery of the fungus was obtained from wood with a 35 to 40 percent moisture content. There were some indications that factors associated with the passage of time may also limit the survival of the fungus in wood. The wood rays were apparently the principal avenue of fungal invasion; breakdown of the wood was not apparent as a result of such invasion. No sporulation of the organism in the interior of wood was noted, although fruiting was frequent on the outer surfaces of blocks.

In general, the study provided additional evidence that the oak wilt fungus can survive in oak wood and that it conceivably might be carried in oak products.

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Colchicine-Induced Polyploidy in Abies

BY
FRANCOIS MERGEN
DONALD T. LESTER

THE GENETIC AND CYTOLOGICAL ASPECTS of members of the genus *Abies* have received virtually no attention. Besides the determination of the chromosome number, little information has accumulated on either their normal or abnormal cytology. As part of a broad study on the genetics of *Abies*, the compatibility between the various members, the karyotypes of individual species, the cytology of microsporogenesis, and the response to colchicine are being investigated. In this report are presented the results of experiments on the effect of colchicine on germinating seed and young seedlings of 9 species of *Abies*. The main objective of the study was to obtain information on the effectiveness of colchicine as a chromosome-doubling agent in *Abies*, and also to obtain polyploid *Abies* seedlings for further work. To obtain a representative sample of this genus, and a good range in seed sizes, seed or plant material from the following species were used: *Abies balsamea* (L.) Mill., *Abies alba* Mill., *Abies concolor* (Gord.) Engelm., *Abies guatemalensis* Rehder, *Abies grandis* Lindl., *Abies lasiocarpa* (Hook.) Nutt., *Abies Nordmanniana* (Steven) Spach., *Abies procera* Rehd., and *Abies sachalinensis* Mast.

In the Pinaceae, polyploidy has been induced by treatment with colchicine in *Pinus* (Mirov and Stockwell 1939, Kiellander 1950, Zinnai 1953, Hyun 1954, Mergen 1959), *Picea*, and *Larix* Kiellander 1950, and Illies 1952). Although doubling of chromosomes was achieved, the resulting trees were physiologically and morphologically depressed, and were inferior to the diploid controls in their overall growth pattern. A review of the literature on polyploidy induction in forest trees was recently published by Mergen (1959), and will therefore not be reviewed for this report. To the authors' knowledge no reports on the effect of colchicine on *Abies*, nor findings of abnormal or polyploid *Abies*, have appeared in print.

Material and Method

It is well established that the mutagenic effect of colchicine is restricted to dividing cells. More specifically, it acts on the spindle fiber mechanism during cell division and arrests the normal movement of the chromosomes after metaphase. Consequently colchicine treatments are effective only on actively dividing cells, and the treatment methods and schedules used were chosen so that the plant material would be in a favorable state. The plant material was kept under conditions conducive to cell division during the treatment. Three types of material were used: (1) seed, (2) freshly germinated seedlings, and (3) one to 12-month-old seedlings.

Before the seed was treated, it was stratified for 1 to 3 months so that the germination process would be speeded up and more uniform once the seeds were placed in a colchicine-enriched medium. The seed was treated in Petri dishes by placing the seed either on filter paper, or mixing it with peat moss or fine quartz sand moistened with aqueous solutions of colchicine. The Petri dishes were kept under normal room conditions and did not receive any specific

The authors are with the School of Forestry, Yale University, New Haven, Conn. The work reported here is being supported by a grant from the National Science Foundation (G-8891). Manuscript received Oct. 3, 1960.

light treatments during the treating period.

The freshly germinated seedlings were placed in specially prepared dishes so that the cotyledons and plumule were covered with cheese cloth soaked in colchicine, while the elongating radicles were placed in water. This was done to minimize the deleterious effect of colchicine on the developing radicles. Another method consisted of placing the freshly germinated seedlings in fine quartz sand that had been moistened with colchicine, and then covering them completely with sand.

The older seedlings were treated by bringing the apical growing point into contact with the colchicine solutions. Various methods were used, such as submerging the tip of the seedling in a vial containing aqueous colchicine, placing cotton balls soaked in colchicine on either intact or "clipped" terminal growing points, or by sealing the growing point into a small glass tube that was kept filled with colchicine solution. During the treatment the seedlings were kept under favorable photoperiods (17 hours) and high light intensity. The treatment period varied between one and five days.

Besides these treatments, modification of these techniques, such as treatment under vacuum at higher temperatures, injection into the growing points, or treatment with a colchicine-enriched lanolin paste, were tried.

The various treatments were allocated according to the plant material that was available and in the proper growing condition at the time.

Results and Discussion

The results of treatment effects are summarized in Table 1. A comparison of these results with those obtained with *Pinus elliottii* and other members of the genus *Pinus* indicate a much lower effect of colchicine on *Abies*. It is difficult to isolate the factor or factors that caused this low effect. *Abies* seed has a notoriously low germinative capacity as a result of dormancy of the embryos, injuries incurred during dewinging, insect infection, and the overall perishable nature of the seed (Anonymous 1948). Therefore in the seed treatments, the low effect could have been caused by the treatment technique, or the low overall germination capacity, or both, rather than the plant's mitotic insensitivity to colchicine. However, in the treatment of seedlings, colchicine was brought in contact with dividing cells that were under favorable conditions for further division, which would indicate a low sensitivity to colchicine. The results also brought forth the fact that the method of treatment has a great effect.

The seeds that germinated in treated peat moss or filter paper did not show the abnormalities of swollen radicle or hypocotyl; nor did they exhibit the ball of tissue at the tip of the radicle that is characteristic of pine seedlings germinated in a colchicine-enriched medium (Mergen 1959). Under both conditions of germination the radicles grew very slowly and were heavily attacked by microorganisms even after the seed had been surface-sterilized with sodium hypochlorite. The greatest number of abnormal seedlings was obtained when seed was germinated in quartz sand saturated with a 0.4 percent aqueous solution of colchicine. Most of the seedlings showed some degree of abnormality, and the fungus invasion was also minimized by this treatment. Of the seedlings thus obtained only *Abies Nordmanniana* showed no visible effect. Representative abnormal seedlings of *Abies balsamea* after they had germinated on sand are illustrated in Figure 1A.

Of the methods used on freshly germinated seedlings, treatment in quartz sand was the only successful method. The *Abies alba* seedlings so treated showed the typical colchicine effects (Fig. 1B), and attempts to save these seedlings by micro-grafting them onto normal diploid seedlings failed.

The treatment of the older seedlings resulted in occasional abnormalities, and they

TABLE 1. Summary of treatments and results.

Species	Type of material	No. treated per concentration	Concentration (Percent)	Method	Results
Abies balsamea	Seed	20	0;0.05;0.1;0.2; and 0.4	Shredded peat moss	18 germinated; 3 abnormal
Ditto	Seed	50	0.4	Fine quartz sand	10 germinated; 10 abnormal
Abies alba	Seed	50	0.4	Fine quartz sand	2 germinated; 2 abnormal
Ditto	Freshly germinated seedlings	20	0.4 and 0.8	Fine quartz sand	5 abnormal
Abies concolor	Seed	20	0.0;0.05;0.1;0.2; and 0.4	Shredded peat moss	17 germinated; 6 abnormal
Abies guatemalensis	One-year-old seedlings	6	0.4	Apical growing points submerged for 8 hours	No visible effect
Abies grandis	Seed	50	0.4	Fine quartz sand	6 germinated; 6 abnormal
Ditto	Freshly germinated seedlings	25	0.2;0.4; and 0.8	Apical growing points covered with cheesecloth moistened with colchicine for 3 days	No visible effect
Ditto	One-month-old seedlings	30	0;0.4; and 0.8	Cotton placed on apical growing point for 1, 3, and 5 days	6 abnormal
Abies lasiocarpa	Seed	15	0;0.025;0.1;0.2; 0.4;0.8;1.0; and 2.0	Filter paper	No visible effect
Ditto	Two-month-old seedlings	3	0.2;0.4; and 0.8	Top placed in solution for 3 days	No visible effect
Abies Nordmanniana	Seed	50	0.4	Fine quartz sand	No visible effect
Abies procera	Seed	20	0;0.05;0.1;0.2; and 0.4	Shredded peat moss	16 germinated; 6 abnormal
Abies sachalinensis	Seed	20	0;0.05;0.1;0.2; and 0.4	Shredded peat moss	19 germinated; 4 abnormal
Ditto	Seed	50	0.4	Fine quartz sand	8 germinated; 6 abnormal

formed short and thick needles during the first flush of growth after treatment (Figure 1, C and D). These needles had the typical bluish hue that was observed in polyploid pines, but cross sections through these abnormal needles revealed no structural abnormalities, although the outer shape was abnormal and irregular. However, none of the subsequent flushes of growth produced abnormal needles.

The degree of polyploidy varied between tetraploid and octoploid +, and the highest *verified* chromosome number (8n) was found in cells of a needle base of *Abies balsamea*. This particular seedling had been germinated on sand that was treated with colchicine. Although much higher polyploid numbers were observed, their precise number could not be established. An example of this is illustrated in Figure 1. F and G where metaphase of a polyploid *Abies balsamea* cell is represented. Figure 1F is an enlarged view of two of these chromosomes to show their double condition. The effect of colchicine on chromosome movement was similar to that reported for *Pinus* and other plant species, and the typical "C-pairs" were observed in a large number of cells. A representative illustration of this type is given in Figure

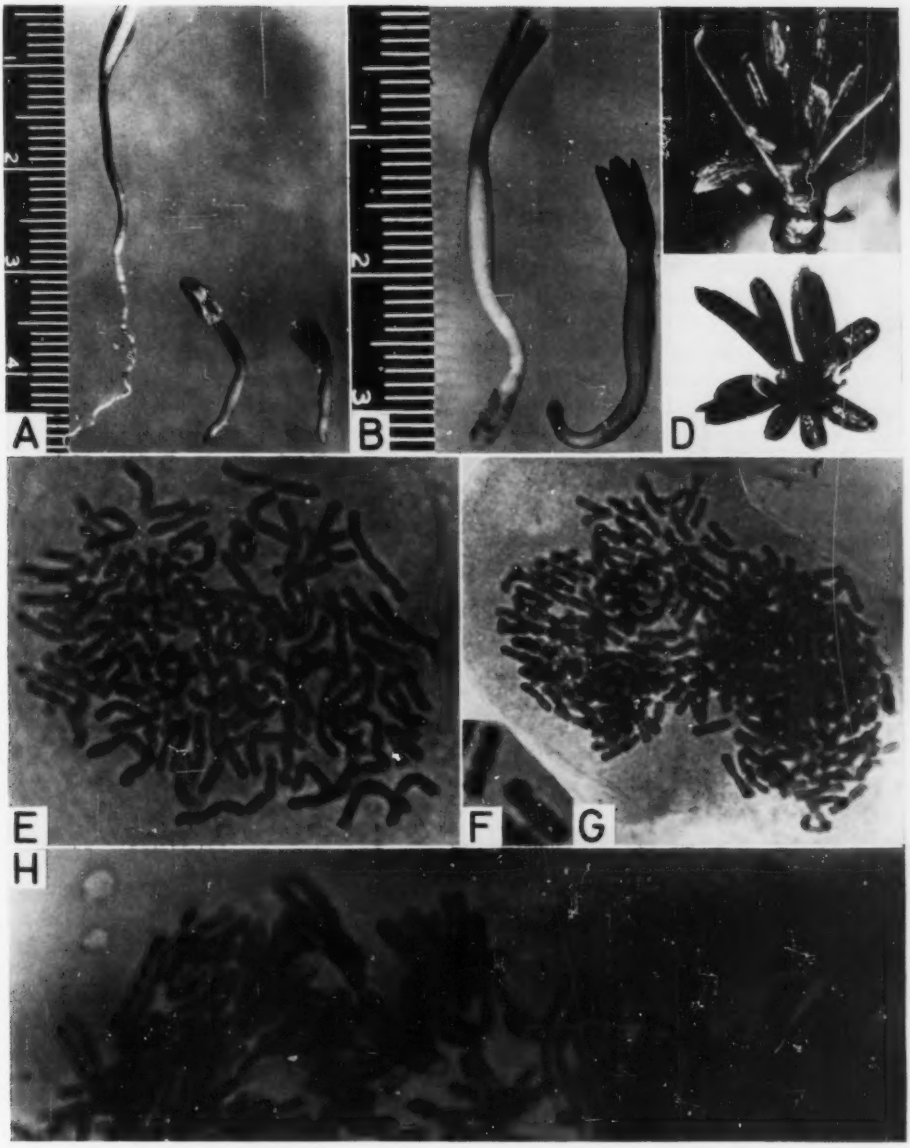

FIGURE 1. *Reaction of* Abies *seedlings to colchicine. A. Seedlings of* Abies balsamea *germinated in sand treated with (L to R) 0.0 percent, 0.4 percent, and 0.8 percent colchicine. B.* Abies alba *seedlings placed in sand soaked with 0.8 percent colchicine. C and D. Swollen primary needles of* Abies lasiocarpa *seedling after treatment of apical meristem with 0.4 percent colchicine. E. Octoploid (8n) cell of* Abies balsamea, $\times 1100$. *F and G. Metaphase chromosomes of polyploid cell of* Abies balsamea, $F = \times 1500$, $G = \times 650$. *H. Anaphase in polyploid cell from root tip of* Abies balsamea, + *2100.*

1H, where the chromosomes have separated after doubling and have the appearance of pairs of skis.

The low incidence of visible effect from colchicine treatment is of great interest. Aceto-carmine smears were made of a large number of treated seedlings, and in some instances polyploid cells were observed in seedlings or tissue that had no abnormal appearance, while in abnorn al seedlings the cells in the swollen tissues showed no abnormality. Illies (1951), in observing similar conditions in colchicine-treated seedlings of spruce and larch, postulated that this discrepancy between the morphological and cytological condition might be caused by the number of polyploid cells that are present. In a shoot that appears "diploid" on the basis of its external morphology the proportion of diploid cells might be greater, while in "polyploid" shoots the number of polyploid cells would be larger. To explain the condition in a spruce seedling with "polyploid" appearance that did not have any actively dividing polyploid cells, Illies cited the observations made by Hertzsch (1951) on *Vicia*. In these plants a reversion from a polyploid condition to a lower number had taken place in the C_1 generation, and this change did not reduce the size of the cells and these plants maintained a larger cell volume. Therefore, she felt that in plants where this reversion to diploidy occurs in the same plant without going through a sexual reproduction process, the enlarged cell size could very well be maintained. However, we feel that more work of a detailed nature has to be done to explain the discrepancy between the external morphological appearance and the cytological condition of the plants.

From the evidence of the small number of polyploid *Abies* seedlings that were obtained, and from their rapid reversion to a diploid state, it appears that the polyploid cells are not capable of competing with the surrounding diploid cells and are swamped rapidly by the physiologically more active diploid tissue. This is not a reversion of polyploidy to diploidy within individual cells, but a more rapid division and growth of diploid cells.

Treating the shoot apices with colchicine had little effect beyond stopping the growth during treatment and for some time after the colchicine solution had been removed. No polyploid tissue that was able to continue growth as such was obtained.

The induction of polyploidy as evaluated by the frequency of abnormal plants was not related to the concentration of colchicine used in a particular treatment. Apparently, the physiological condition of the cells was of greater significance than the concentration.

At the conclusion of the study, after two growing seasons, no polyploid *Abies* seedlings are still alive. The death rate due to microorganisms was much greater than that found in *Pinus elliottii*, and surface sterilization was only moderately effective. This is quite contrary to the results that were obtained with *Pinus elliottii*, of which a considerable number of polyploid seedlings are still growing after four growing seasons. In addition, the technique that was most successful with *Pinus elliottii* (peat moss) was not very successful with *Abies*, possibly because this medium provided a favorable condition for the microorganisms.

Summary

Seeds and plant material of 9 species of *Abies* were treated with aqueous colchicine solutions (0.025-2.0 percent) in an effort to obtain polyploid individuals. The most successful treatment consisted of burying freshly germinated seedlings in fine quartz sand that had been moistened with 0.4 percent colchicine. Although seedlings with polyploid cells were obtained, these cells were unable to compete with diploid tissue. The results are summarized in tabular form, and are illustrated with photographs.

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An Annotated Bibliography on the Uses of Statistics in Ecology—A Search of 31 Periodicals

By Vincent Schultz. U.S. Atomic Energy Commission. Environmental Sciences Branch, Washington, D.C. 315 pp. 1961. $3.

Review by John W. Duffield
Industrial Forestry Association
Nisqually, Washington

This literature search covers 25 ecology and 6 statistics periodicals from their first issues through 1958. General subject fields used in grouping the references are: wildlife, fisheries, limnology and oceanography, plants, insects, and miscellaneous. Forestry is not given as a field, but FOREST SCIENCE is covered. Under each of these subject fields each periodical is analyzed as follows. First is an index of statistical concepts, terms, etc. giving volume, number and page references. Examples of these headings are: assumptions, descriptive statistics (with numerous sub-classes), probability, sampling, transformations. This index is followed by full references to each paper indexed for the journal. The 6 statistics periodicals are not listed in this section, but in a separate one of 11 pages, without detailed topical references.

Two indexes are provided: a brief one which lists the pages in the bibliography on which each periodical is mentioned, and one on statistical usage, broken down by the subject fields, but grouping page references to all the periodicals dealing with this field.

This work should be available to all research workers in forest science.

Soil-Site Studies in Piedmont Hardwood And Pine-Hardwood Upland Forests

BY
LINO DELLA-BIANCA
DAVID F. OLSON, JR.

THE RESEARCH DESCRIBED here is part of a comprehensive study of the relationship of soil and topography to the height growth of yellow-poplar (*Liriodendron tulipifera* L.), white oak (*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.), and shortleaf pine (*Pinus echinata* Mill.) in the uplands of the Virginia-Carolina Piedmont. The first phase of this study compared the site index of these tree species when they occur on the same site (Olson and Della-Bianca 1959). The concluding phase, to be published later, will present the associated chemical and hydrologic properties of the soils.

Description of the Region

The Piedmont Plateau is one of the major physiographic divisions of the United States and extends southwestward from the Potomac River through the South Atlantic states into Alabama. The land surface is characteristically flat to gently rolling. Small mountains, such as the Uwharries, rise up from the peneplain in several places; these were bypassed in this study because environmental conditions are not typical of the Piedmont.

The Piedmont has a very favorable climate for forest growth because of a humid, frost-free growing season lasting from 204 to 228 days. Annual precipitation ranges from 40 to 48 inches, practically all of which is rainfall. The mean annual temperature varies from 56° to 61°F; July temperatures are warmest with an average maximum of 87°F.

With few exceptions the upland vegetative communities are of secondary origin and have developed on abandoned agricultural fields. The stages of old-field succession in the Piedmont uplands are distinct and have been described by Oosting (1942). Forbs and grasses, especially broomsedge, are dominant until about the fifth year after land abandonment. Then pine seedlings gradually assume dominance and eventually establish continuous stands. After about 40 years a mixed-hardwood understory develops and assumes increasing importance as the pine stands mature and thin naturally. In 150 to 200 years the pine is replaced, except for scattered relicts, by the climax oak-hickory forest (Fig. 1).

Piedmont soils are in the red-yellow podzolic group. In general, these soils have relatively thin organic and organic-mineral layers over a yellow-brown leached, mineral layer underlain by a red or yellow subsoil. Because of the extreme age of Piedmont formations, soils and weathered rock of considerable depth are found in some places. Gullied areas often reveal weathering to depths of 30 to 40 feet. Lee (1955) presents a comprehensive system of Piedmont soil classification.

Few examples can be found of virgin

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Piedmont soils as they occurred when settlement began. Past land use has decimated the soil resource. Vast areas have been subjected to soil erosion which ranges from persistent barrens to gully systems spreading over scores of acres. All land-use functions are impaired wherever erosion exists.

The portion of the Piedmont covered by this study includes the uplands of North and South Carolina, and those of Virginia south of Buckingham County. The commercial forest land, occupying 60 percent of the land area, is distributed among some 200,000 small woodland owners. Upland hardwoods and pine-hardwoods cover 6.5 million acres, 3.1 million acres are in shortleaf pine, and other forest types occupy some 4.2 million acres. The acreage of upland hardwoods is increasing because natural succession in the region results in an oak-hickory climax. Intensive fire protection and heavy cutting of pine have aided hardwood encroachment.

Review of Selected Literature

In the past 30 years, 65 articles have been published concerning the soil-site relationships for various tree species throughout the United States. A number of techniques have been used for expressing study results, but within the last decade there has been an increasing use of regression analysis. Some soil-site studies have been done for the tree species included in this Piedmont study; with the exception of shortleaf pine, they pertain to other geographical regions.

Soil-site studies for oaks over a variety of geographic provinces and climatic conditions have produced prediction equations with very similar soil and topographic factors, slope (position and/or percent), soil depth (either depth of A horizon or total depth), and aspect or some factor confounded with it such as percent sand in the A horizon (Gaiser 1951a, Einspahr and McComb 1951, Trimble and Weitzman 1956, Doolittle 1957). Gysel and Arend (1953)

FIGURE 1. *A Piedmont timber stand representing the climax oak-hickory forest.*

also found slope expressions significant, but their other important criteria included subsoil texture and moist substrata layers within 4 to 10 feet of the surface. Arend and Julander (1948), in the Arkansas Ozarks, found soil depth significant; however, their only other significant factor was parent material, with soils of limestone origin having a higher productivity than those of sandstone or shale origin.

The oak study by Doolittle was confined to a single watershed whereas that by Trimble and Weitzman included four counties. These studies accounted for 95.7 and 74 percent of the variation in site index, respectively. Hodgkins (1956), in testing the applicability of soil-site index tables in predicting the site index of loblolly, longleaf, and slash pine in southwestern Alabama, concluded that the tables of highest utility are those designed for small geographic areas with distinctive soil conditions and uniform climates. The difference in accountable site index variation shown by the oak studies of Doolittle and those of Trimble and Weitzman serves to support Hodgkins' conclusion about the importance of area limitation.

In the lower Piedmont of North Carolina, site index of shortleaf pine is influenced by the thickness of A horizon and physical properties of the subsoil (Coile 1948). The subsoil properties are the ratio of silt plus clay to the moisture equivalent, and the imbibitional water value. These two subsoil properties are indices of soil friability, moisture relations, and internal drainage; as they indicate better soil porosity, site index of shortleaf pine increases. Site index increased in going from ridge to bottoms, but this was confounded with depth of surface soil.

Soil aeration and internal drainage conditions are influenced by the amount and characteristics of subsoil clay (Coile 1952, Zahner 1958); they can seriously impede tree growth if not adequate, and may even cause serious pathological problems (Copeland and McAlpine 1955).

Zahner (1958) showed that a curvilinear relationship exists between the site index of shortleaf pine and surface soil thickness and clay content of the subsoil for mature upland soils in northern Louisiana and southern Arkansas; site index reaches maximum at medium values of surface thickness and subsoil texture; site index decreased with increases of slope.

Auten (1945) considered the depth of topsoil above tight subsoil as the most important factor in evaluating site for yellow-poplar; the greater this depth the better the site. The thickness of A_1 horizon was considered useful as a site indicator for the species, but insufficient without consideration of depth to tight subsoil.

All cited studies have emphasized the importance of some form of soil depth in predicting site index. However, studies of soil-site index of white pine in the Northeast showed a negative correlation between site index and total A horizon depth (Young 1954) and A_1 horizon thickness (Foster 1959).

Ovington and Madgwick (1959) maintain that if litter and humus breakdown can be stimulated, large amounts of plant nutrients would become available to the trees. Recently, Walker and Reed (1960) found negative correlations between height growth of catalpa (*Catalpa speciosa* Ward), a site-sensitive species, and organic matter in mineral soil. This was considered as a trailer effect of an unfavorable relationship between silt plus clay and general stand growth; furthermore, the surface foot of soil was considered as more important in determining site index than the deeper layers of soil. Earlier, Coile (1952) reported a negative correlation between the site index of pond pine (*Pinus serotina* Michx.) and the interaction of depth A_1 x organic matter. This was for mineral soils with up to 15 percent organic matter in the surface soil. In the case of pond pine, excessive amounts of organic matter may reflect poor drainage, a direct cause of low productivity.

Methods

Field. Plots from 1/5- to 1/2-acre in size were established in 153 upland forest stands ranging from 500 to 900 feet in elevation. Study areas were located so that the plots would be homogeneous with respect to soil type, litter cover, topography, aspect, and degree of slope. Only well-developed stands, ranging from 30 to 100 years old and showing no evidence of fire, grazing, erosion, or destructive cutting, qualified for selection. On each plot an aggregate of four dominant and codominant trees of as many species as possible was selected. Total height and total age were determined for each tree and the data averaged by species. A 10-year limit was placed on the range of ages for trees of the same species within a plot. Sound trees were chosen which were reasonably similar as to crown size, bole form, and diameter. Each plot contained either yellow-poplar (98 plots), white oak (97), or shortleaf pine (101), singly or in mixture; scarlet oak (54) and black oak (59) were often included as well as other upland tree species.

Soil pits were dug at the plot center and distributed in each 120 degree segment according to the method proposed by Gaiser (1951b). The thickness of both the litter and fermentation layer was recorded along with the approximate pine and hardwood litter percentages and root concentrations. The thickness of the A_1, A_2, and B_1 horizons was measured for each pit, as well as the depth to the B_2 soil horizon. A one quart soil sample of each of the four horizons was collected from each soil pit.

Physiographic data recorded for each plot included slope percent, aspect, slope position and landform.

Laboratory. All soil samples were air-dried, rolled, and passed through a 2-mm sieve. The samples used for the organic matter determinations of the A_1 soil horizon were reduced with a mortar and pestle and passed through a 0.5 mm sieve. The organic matter determinations were done by the wet-combustion method proposed by Chesnin (1950). The method has been checked against the method by Peech *et al.* (1947) with good results.

Soil texture was determined by the hydrometer method (Bouyoucos 1951). A pressure membrane apparatus was used to obtain percent moisture in the soil at 15 atmospheres of pressure by the procedure developed by Richards (1947). A soil centrifuge was used to determine the moisture equivalent and xylene equivalent values (Briggs and McLane 1907). The imbibitional water value was computed as the difference between moisture equivalent and xylene equivalent (Coile 1948).

The four soil samples from each horizon within each plot were processed independently for the physical properties determinations and then averaged to obtain plot values. The organic matter determination for the A_1 soil horizon in each plot was based on a pair of samples drawn from a composite of all the A_1 samples of the plot.

Analysis and Results

After summarizing all the field and laboratory data, scatter diagrams were constructed for each species by plotting the appropriate site indices over each of 63 soil and site factors. Site classification was based on equations of the form,

$$\text{Log total height} = a + b\left(\frac{1}{\text{Total age}}\right)$$

using the height and age data obtained on the comparative site index plots reported earlier by Olson and Della-Bianca (1959).

In general, the following variables were tested by using various soil horizon combinations and appropriate interactions: soil separates, soil horizon thicknesses, moisture equivalent, wilting point, available water, stoniness, and imbibitional water values. The site factors considered were: slope position and percent, latitude and longitude,

and various expressions of aspect. In addition, the mean annual d.b.h. growth of dominant and codominant trees was analyzed by individual species; no satisfactory correlations were obtained.

The selection of variables used in the initial multiple regression was made on the basis of the plotting and further tests of promising factors by computing single variable regressions to determine significance by the F-test.

To express the basic height-age relationship that defines the master site curve of each tree species from its soil-site equation, the logarithm of total height, rather than log site index, was used as the dependent variable with the reciprocal of total age as the first independent variable. This approach avoids any assumption that the forms of the height-age curves are constant for all combinations of soil and site data. The basic soil-site equation becomes:

$$\text{Log total height} = b_1 + \frac{b_2}{\text{Age}} + b_3X_3 + b_4X_4 \ldots + b_nX_n$$

Fifteen of the most promising soil and site factors were selected, and five multiple regression analyses were made. The following list presents the arrangement.

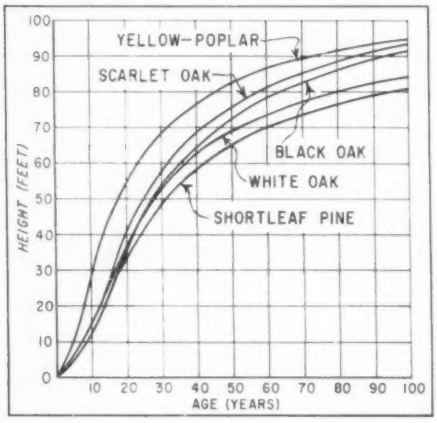

FIGURE 2. *Mean height-age curves based on soil-site equations for Piedmont upland species in mixed timber stands.*

Dependent variables

Y_1 —Logarithm of total height (yellow-poplar)
Y_2 —Logarithm of total height (white oak)
Y_3 —Logarithm of total height (shortleaf pine)
Y_4 —Logarithm of total height (scarlet oak)
Y_5 —Logarithm of total height (black oak)

Independent variables

X_1 —Unit weight
X_2 —1/Total age
X_3 —Slope position, percent distance ridge to stream (Ridge=0; stream=100)
X_4 —1/Thickness of A_1 horizon
X_5 —Percent of organic matter in A_1
X_6 —Percent of organic matter in A_1 x thickness of A_1
X_7 —1/Thickness of total A horizon
X_8 —1/Depth to B_2 horizon
X_9 —Imbibitional water value of B_2
X_{10}—Percent sand in A_2
X_{11}—Percent sand in A_2 x thickness of total A
X_{12}—Imbibitional water value of B_1
X_{13}—Imbibitional water value of B_2 x thickness of total A
X_{14}—Aspect, as sine of azimuth from SE+1
X_{15}—Slope percent
X_{16}—Longitude, in degrees and hundredths
X_{17}—Latitude, in degrees and hundredths

The coefficient of multiple determination, R^2, was computed for each of 575 equations by individual tree species. This represented all possible combinations of 2, 3, and 4 variables with the restriction that each contain the reciprocal of total age as one of the variables. Then step-wise analyses were done using each remaining variable in turn, to determine if significant improvements could be obtained over the best regressions found in the initial screening. After the significant variables had been isolated for each tree species, regression equations were computed using these variables. Plotting the residuals of these equations revealed no departures from linearity.

Optimum equations. The equations presented here represent the statistically best equations derivable from the complex of soil and site factors tested. The mean height-age (site index) curve for each tree species is shown in Figure 2; the average

TABLE 1. Variation in total height accounted for by significant regression factors, in optimum equations.

Species	Total age	Soil factors	Latitude and topographic factors	Total
		Percent[1]		
Yellow-poplar	27.0	6.5	23.0	56.5
White oak	38.8	5.8	11.2	55.8
Scarlet oak	41.9	2.6	20.9	65.4
Black oak	49.1	3.2	3.5	55.8
Shortleaf pine	63.1	8.5	4.5	76.1

[1]Computed as a ratio of the sum of squares for the appropriate factor to the total sum of squares.

site index by individual species is the appropriate height represented at age 50 years. For white oak, scarlet oak, and shortleaf pine, it was possible to develop alternate equations that substitute the percent sand in the A_2 horizon for organic matter; however, there was some loss in accuracy.

Yellow-poplar:

$$Y_1=0.42027-6.02173X_2 +0.00098X_3+0.00146X_6 +0.40356X_7+0.00011X_{11} +0.04114X_{17}$$

White oak:

$$Y_2=2.03665-8.63679X_2 +0.00069X_3-0.00313X_5$$

Shortleaf pine:

$$Y_3=2.03127-9.44367X_2 +0.00087X_3-0.00352X_5$$

Scarlet oak:

$$Y_4=2.05136-8.89124X_2 +0.00068X_3-0.00263X_5 +0.00217X_{15}$$

Black oak:

$$Y_5=2.07996-10.12808X_2 -0.00305X_5+0.00195X_{15}$$

The importance of age, soil factors, and topography and latitude, as computed from the analyses of variance for each regression, is presented in Table 1. For all species except yellow-poplar, total age of the trees accounts for a far greater proportion of total height variation than the soil-site variables. For yellow-poplar slightly less than half of the height variation accounted for in the equation is a function of age. The high sensitivity of yellow-poplar to changes in site is evident from these results.

Discussion

All of the analyses show that the accepted method of correlating site index with permanent features of the land has only been partially successful in these mixed stands. There are logical reasons for this. First, the correlations had to be made for select stands which did not contain very shallow, or gullied soils, both very common Piedmont soil conditions. Second, existing techniques for identifying and measuring the complex of soil and site factors may not be precise enough to detect minor but significant differences in these factors. And last, the study was conducted over a broad geographical area containing many soil types. This is in contrast to hardwood studies by Doolittle (1957) and Trimble and Weitzman (1956), where better correlations were obtained on restricted areas of limited soil variation.

The results of this study are applicable only to undisturbed hardwood or pine-hardwood forests, or to recently cutover land which was formerly stocked with similar stands. These results should not be extended to include recently abandoned fields or severely disturbed woodlands. In view of the restricted applicability of any of these results, soil-site equations from this paper should be used with caution. Broad application on all classes of Piedmont land could lead to erroneous and optimistic

conclusions. Actually the limitations imposed by the results are such that direct stand measurements of site index or volume production would be preferable for obtaining a site index or productivity estimate.

Notable successes with soil-site prediction for several species of southern pine over wide areas are reported by Coile (1952) in a paper summarizing the efforts of several researchers. However, like the work reported here, many show relatively little of the height growth variation accounted for by soil-site factors. They have been useful primarily because the southern pines are pioneer species that develop thrifty stands on abandoned fields and recent burns. Accordingly, the soils studied in pine soil-site investigations are much more comparable to open land conditions than soils in mixed pine-hardwood and hardwood stands.

Except for a weak correlation of soil thickness variables with yellow-poplar site index, soil thicknesses were not correlated with the site index of any other tree species in this Piedmont study. For these mixed stands in the Piedmont only a few impervious subsoils were found, and as Table 2 shows, the differences in average soil depths among average, good, and poor sites are slight. This is in contrast with findings for natural shortleaf pine stands growing on eroded old fields (Coile 1948).

Subsoil properties were not significantly correlated with the height growth of tree species considered in this study; they showed a considerable range in values for both productive and low quality sites. As an example, for the high and low site index groupings for scarlet oak in Table 2, the imbibitional water value for the B_2 horizon ranged from 5.4 to 10.2 percent for the high site index group, and from 4.9 to 11.3 percent for the low group. Similarly, the clay content of the B_2 ranged as fol-

TABLE 2. Some properties of Piedmont soils associated with mean site index and site index extremes.

Species	Site index[1] group		Plots	Organic matter in A_1	Thickness A_1	Depth to B_2	IWV[2] B_2	Soil separates in A_2[3]		
								Sand	Silt	Clay
			Number	*Percent*	*Inches*	*Inches*	*Percent*		*Percent*	
Yellow-poplar	Mean	(83)	98	10.6	2.3	12.9	6.7	54	25	21
	Low	(64)	9	10.9	1.6	11.2	7.1	56	23	21
	High	(108)	8	8.9	3.2	19.4	5.8	55	26	19
White oak	Mean	(69)	97	12.3	1.9	12.6	7.0	53	26	21
	Low	(55)	11	17.8	1.1	10.0	6.6	43	34	23
	High	(84)	5	6.8	3.5	15.0	6.0	57	23	20
Scarlet oak	Mean	(76)	54	13.3	1.8	12.2	7.3	52	27	21
	Low	(63)	12	17.5	1.4	13.1	6.9	42	33	25
	High	(94)	5	9.9	2.4	11.4	7.7	55	24	21
Black oak	Mean	(73)	59	12.6	1.7	12.1	6.9	52	27	21
	Low	(60)	9	16.1	1.4	9.6	7.8	44	32	24
	High	(91)	5	10.1	2.1	10.9	7.5	57	23	20
Shortleaf pine	Mean	(64)	101	12.8	1.9	12.5	7.3	52	26	22
	Low	(49)	9	17.6	1.2	13.6	5.9	46	30	24
	High	(80)	12	7.9	3.4	16.2	6.8	57	23	20

[1]Average height of dominant and codominant trees at 50 years of age.
[2]Imbibitional water value.
[3]According to International size classification: (2.0–0.02 mm)=sand; (0.02–0.002 mm)=silt; (less than 0.002 mm)=clay.

lows: high site index group, 29 to 48 percent; low group, 24 to 63 percent.

This general lack of significance of subsoil properties in evaluating site quality of hardwood stands might be explained by the fact that these soil profiles are more completely developed than those in pine areas. As soil profiles develop along with vegetative succession, perhaps topsoil properties exert increasing influence on tree growth.

Site index in the Piedmont increases as the distance from the ridge increases. Relative position on slope expressed as percent of the distance from a ridge to a permanent stream was the most important soil-site factor influencing tree height growth. It possibly serves as an integrating expression for the soil moisture regime, rate of decay of organic matter, and the microclimate. Only for black oak and shortleaf pine were other site factors of greater importance. The observed effect of slope position occurs independently of soil thickness, as indicated by a lack of correlation between thickness of A horizon and slope position.

Increases in percent slope favor the height growth of scarlet and black oak in the Piedmont uplands and are independent of slope position since slope percent and slope position were not correlated. These oaks commonly occur on the more mesophytic Piedmont sites, as indicated by aspect, regardless of steepness. Both oaks require well-drained soils for good development, and with clay subsoils predominating in the Piedmont, increases in percent slope would improve soil drainage and aeration to the benefit of both species.

In the mixed stands under study, yellow-poplar proved to be an indicator of above-average site index for all species of oak and shortleaf pine. Where yellow-poplar was present, site index for these associated species was 6 to 10 feet greater than in stands without yellow-poplar.

The equations produced by this study for the oaks and shortleaf pine contain a variable percent of organic matter in the A_1 horizon, i.e., the amount of organic matter in a unit volume of soil, with a negative regression coefficient. For these plots the findings indicate that increasing concentrations of organic matter in the A_1 horizon may be a reflection of other soil factors—low pH, thin A_1 horizon, clayey topsoil—recognized as detrimental to forest growth. A possible explanation for this is shown by the regression developed from these data:

$$\text{Log percent organic matter in } A_1 = 1.28207 + \frac{0.20420}{(\text{Thickness of } A_1)} - 0.12288\ (\text{pH of } A_1) + 0.01236\ (\text{percent clay in } A_2).$$

Considering this relationship, it is apparent that a thin A_1 horizon of low pH, underlain by a dense A_2 horizon high in clay content, can be expected to have a large amount of organic matter. Conversely, with the same variables approaching their optimum values, i.e., a thick A_1, pH approaching 7.0, and a friable A_2, organic matter levels are lower.

Several other researchers have reported a negative correlation between organic matter content and site index (Coile 1952, Walker and Reed 1960). In this Piedmont study, the association of high organic matter content with several unfavorable soil conditions is offered as a possible explanation for the negative correlation.

Aspect had no significant effect on the height growth of these Piedmont tree species after the effect of significant variables had been removed. This may be accounted for by the minor relief differences found in the region. Although the height growth of hardwoods was least in the southwest quadrant, there were only a small number of hardwood plots on these warm exposures because of natural ecological conditions that favor pine invasion.

Most soil-site studies have been confined to individual tree species and specific geographical provinces; however, there is evidence that studies of this nature should be even more restrictive as to the amount of area and the kind of conditions they are to represent. By using field and analytical techniques similar to those developed for soil-

site studies elsewhere, this research was confined to well-developed, climax-type forest stands, with relatively uniform soil conditions. The equations which have been developed offer only a partial solution to the problem of predicting the height growth of trees from physiographic and edaphic variables. Additional research is needed for the complex relationships between litter types and their rates of decay, related soil fauna and flora activity, and edaphic factors as they affect the nutrient supply of these climax-type forest stands.

Summary and Conclusions

A comprehensive study of physical soil-site factors affecting site index of five important timber species was conducted in upland Piedmont forests. The trees and soils were sampled in 153 mixed pine-hardwood and hardwood stands representing an advanced stage of ecological development. Yellow-poplar, white oak, scarlet oak, black oak, and shortleaf pine were measured in various overstory mixtures of two to seven dominant species per plot.

Of the 63 soil and site variables considered in initial trials, fifteen promising ones were evaluated in detailed multiple regression solutions for each species. All possible combinations of 1, 2, and 3 soil-site variables were analyzed jointly with total age of trees.

The resulting equations were not strong predicting equations. They indicated that models used for soil-site investigations in subclimax softwood types will not produce useful guides for these climax forests. This is true in the Piedmont because few hardwood stands develop by invasion of open land, but gradually infiltrate into pine forests on soil of above average quality. The use of hardwood-dominated forests in the Piedmont for soil-site study also precludes fire, grazing, erosion, and destructive cutting. Limitations on plot selection imposed by natural development impose a similar limitation on use of the soil-site equations. They cannot be extended to apply to recently abandoned fields and severely disturbed woodlands.

Nonetheless, the findings of this research provide some important facts about forest soil conditions that affect height growth of the species studied. Surface soil conditions and slope position proved to be important gauges of productivity for all five species. Thickness and organic matter content of the A_1 horizon, thickness of the total A horizon, and percent sand in the A_2 horizon were correlated with yellow-poplar height growth. Percent organic matter in the A_1 horizon was negatively related to site index of oak and pine.

Other findings include a positive effect of increase in slope percent on site index of black and scarlet oak, a positive effect of increasing latitude on site index of yellow-poplar, and higher site index for all species when yellow-poplar is present in the overstory.

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Foliar Absorption and Translocation of Phosphorus by Loblolly Pine Seedlings

BY
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THE DEMONSTRATION of the absorption of mineral nutrients by the foliage of forest trees could lead to a practical means of supplying nutrients required in relatively small amounts. In their comprehensive review, Wittwer and Teubner (1959) cited numerous examples of foliar uptake of nutrients by broad-leaved agricultural plants. But relatively little is known about absorption and translocation of minerals when applied to the foliage of conifers. In the experiments described here, experimental data were obtained on the maximum concentration of di-ammonium phosphate which could be applied to the foliage of seedlings of loblolly pine (*Pinus taeda* L.) without visible injury, the amount of phosphorus deposited in or on the needles, and the amount translocated to new growth during a period of 3 to 5 weeks following treatment. Most of the results described here in this paper were obtained on seedlings grown in 1960, but some preliminary work was done on seedlings grown in 1959. The seasonal timing of the tests was the same in both years.

Production of Seedlings and Their Culture Solutions

Seed[1] for this study was obtained from a single mother tree in Jones County, Ga. Seeds were germinated in sphagnum and the seedlings transferred to continuously aerated water cultures containing the nutrients listed in Tables 1 and 2 for the pretreatment period. The transfers were made daily during the germination period until 24 crocks of 6 seedlings each were filled. The germination period extended from April 4 to April 11, 1960.

The containers used for the water cultures were 14-quart polyethylene buckets, placed inside of 5-gallon crocks for protection from sunlight and for mechanical support. Seedlings were suspended in "styrofoam" plugs set in holes in opaque black plexiglass covers ⅛-inch thick. The plugs were about 1 inch in diameter, which was an ample allowance for the increase in stem diameter of the seedlings during their 5 months under these conditions.

On July 5 when the seedlings were approximately 3 months old, all of them were transferred to culture solutions containing no phosphorus. This solution is identical with that described for treatments I, IV, and V in Tables 1 and 2. After 4 weeks on this minus-P solution, the phosphorus concentration of the secondary needles was reduced to about 0.13 percent of the dry weight of the needles. This level approaches the sufficiency level for phosphorus in loblolly pine needles observed by Fowells and Krauss (1959) to be about 0.10 percent.

Foliar Treatment

Wittwer and Teubner (1959) report greater absorption of phosphate by bean leaves from solutions of H_3PO_4 adjusted to pH 2 and 3 with NH_4OH than with $(NH_4)_2HPO_4$ at pH 7 and 8. Eggert *et al.* (1952), however, obtained better absorption of phosphate by apple leaves from

[1] The seed was supplied by John Barber, U.S. Forest Service, Southeastern Forest Experiment Station, Macon, Ga.

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$(NH_4)_2HPO_4$ than from $(NH_4)H_2PO_4$. The di-ammonium salt provides a good supply of N as well as HPO_4 and thus might have a more favorable effect on growth even if absorbed in a lesser quantity by pine seedlings. For this reason, $(NH_4)_2HPO_4$ was selected for use in the study described here.

Treatment of the foliage was accomplished by immersion. Sprays were not used because of the possible radiation hazard involved in spraying solutions containing the chemical[2] P^{32}. In a preliminary test made in 1959, the need for a wetting agent in the solution was established. When the foliage was dipped in a pure solution of di-ammonium phosphate, no wetting was visible. Satisfactory wetting was obtained, however, by adding 10 drops of "Tween 20" to each liter of solution. This was done on all solutions used for foliar dips.

To prepare seedlings for a foliar application of ammonium phosphate, the seedlings were removed from the culture solution and their root systems were covered with wet paper towels. Treatment consisted of immersing the foliage and stem in a 1-liter cylinder containing a solution of $(NH_4)_2HPO_4$.

About 5 seconds was required for inserting a seedling into the cylinder containing the solution and then removing it. After immersion, seedlings were suspended upside down until the excess solution had drained off. Draining was facilitated by gently tapping the needles with a glass rod. After drainage was complete, the seedlings were returned to their culture solutions in the greenhouse.

Needles of seedlings dipped into solutions of $(NH_4)_2HPO_4$ in concentrations up to 0.51 M (68 gms/L) showed very little damage following treatment. One higher concentration 0.77 M, was tested in 1959, but caused browning of the distal ends of some needles within 3 days after treatment. A concentration of 0.5 M, therefore, was selected for use in the absorption and translocation experiment. This is considerably higher than the 0.03 M solution reported by Tukey *et al.* (1956) as being most desirable for stimulating the growth of bean plants.

To compare the uptake of phosphorus from a foliar application with that from a solution through the root system, a series of 5 treatments was started on August 2, 1960, as follows:

I. No P in either culture solution or on foliage.
II. 50 ppm of P in culture solution and about 0.5 μc P^{32} per liter. Specific activity was about 10 μc per gram of P as of August 2.
III. Same as II but without P^{32}.
IV. No P in culture solution. Tops dipped in 0.5M $(NH_4)_2HPO_4$ containing 0.05 percent "Tween 20" and 900 μc of P^{32} per liter. Specific activity was about 50 μc per gram of P as of August 2.
V. Same as IV but without P^{32}.

The complete composition of the culture solution is listed in Tables 1 and 2. Each treatment was applied to 6 seedlings in each of 4 crocks. Crocks were arranged in a randomized block design in a greenhouse.

Sampling Procedure

Samples of old and new needles were taken from seedlings when growth following treatment had been sufficient to produce new fascicles with a length greater than 5 cm. Sampling on another group of seedlings was made before treatments were started. It revealed that after a needle length of about 5 cm had been reached, phosphorus concentration—expressed as a percentage of dry weight—remained constant with increasing length. Needles less than 5 cm in length, however, had a somewhat higher percentage of phosphorus, as shown in Table 3.

Samples of needles and root tips for treatments II and III were taken 27 days after

[2] The author is indebted to J. E. Leggett, Soil and Water Conservation Division, ARS, U.S. Dept. of Agric., Beltsville, Md., for the P^{32} used in this study.

TABLE 1. Sources and quantities of N and P used in the culture solutions of the five treatments.

Treatment designation	Compound	Concentration	Element	Concentration
		mM/L		*ppm*
Pretreatment	NH_4NO_3	3.57	N	100
	KH_2PO_4	0.16	P	5
			K	6
II and III	$(NH_4)_2HPO_4$	1.61	N	45
			P	50
	$NaNO_3$	3.93	N	55
IV, V, and I	NH_4NO_3	3.57	N	100
			P[1]	0

[1] P was applied to foliage in treatments IV and V.

TABLE 2. Components and concentrations of nutrients, except N and P, used in all culture solutions.

Compound	Concentration	Element	Concentration
	mM/L		Ppm
K Cl	1.28	K	50
$MgSO_4$	1.00	Mg	24
$CaCl_2$	1.00	Ca	40
$FeC_6H_5O_7 \cdot 5H_2O$	.00358	Fe	0.2
H_3BO_3	.0462	B	0.5
$MnCl_2 \cdot 4H_2O$	.0092	Mn	0.5
$ZnSO_4 \cdot 7H_2O$	.000762	Zn	0.05
$CuSO_4 \cdot 5H_2O$	.000315	Cu	0.02
$H_2MoO_4 \cdot H_2O$	.000105	Mo	0.01

treatments were started. For treatment I (no P in solution) and treatments IV and V (foliage dipped), the production of new needles required a longer time and sampling was delayed until 45 days from the time of treatment.

A sufficient number of needles were taken to provide duplicate samples having dry weights between 0.4 and 1.0 gms. The relationship between needle length and dry weight (Table 3) was worked out so that the number of needles needed for a unit of dry weight could be computed before sampling.

Root-tip samples were taken immediately following the collection of needle samples. These samples were obtained by lifting the root systems out of the solution and clipping off the larger white roots at a distance of 10 cm from their tips. Dry weight of these samples was between 0.1 and 0.3 gms. The film of culture solution adhering to the external surface of these segments was diluted or removed by rinsing with 3 portions of distilled water. Total immersion time during this rinsing procedure was less than one-half minute. No check was made on possible leaching of phosphorus from the root tips during the rinsing.

Sample Preparation and Analytical Procedures

The samples of needles and roots were placed in 50-ml Pyrex beakers and dried at 70° C for 24 hours. Weighed samples

TABLE 3. Relationship between length, dry weight, and phosphorus content of needle fascicles of loblolly pine seedlings.

Length class	Median length	Ovendry fascicle weight[1]		Total phosphorus content	
		Total	Per cm of length	Per unit dry weight	Per fascicle
Cm	*Cm*	*Mg*	*Mg*	*Percent*	*Mg*
<2.5	—	—	—	.15[2]	—
2.6-5.5	4.0	9.0	2.3	.14	0.013
5.6-8.0	6.8	17.0	2.5	.09	0.016
8.1-10.5	9.2	26.3	2.8	.10	0.027
10.6-13.0	11.8	33.1	2.8	.10	0.033
13.1-15.0	14.2	39.7	2.8	.09	0.037

[1] All fascicles contained 3 needles.
[2] Dry weight includes both needles and stem.

of ovendried material were ashed in a muffle furnace at 500° C for about 4 hours following the procedure described by McAuliffe (1949) with some modification. About 10 ml of 8 N nitric acid was added to each sample and evaporated to dryness. On some samples, this nitric acid digestion was repeated 2 or 3 times to complete the destruction of organic matter.

Samples used for determination of radioactivity tagged phosphorus (P*) were then dissolved in 2.00 ml of 2 N nitric acid. Complete dissolution of the ash was not obtained on all samples with this volume of acid, but the presence or absence of suspended material in the solution did not affect the precision of the radioactivity measurement. Aliquots of 500 micro-liters were pipetted into stainless steel planchets, evaporated to dryness under a heat lamp, and counted in a gas-flow proportional counter. Activity in each sample was measured in terms of the time, minutes ± 0.01 min., required for 3000 counts. Activity was converted to mg of P by a calibration curve plotted from the activity of known quantities of $(NH_4)_2HP^*O_4$ having the same specific activities as used in the culture solution and in the solution used for immersing the foliage.

A comparison was made of the counts on standard planchets prepared with and without the approximate ash content for a particular P content, and no consistent differences in counting time were detected. Self-absorption of β radiation on the ash apparently was thus not a source of detectable error, so all standards were prepared by adding sufficient 0.5 M. $H_3P^*O_4$ to solutions of $(NH_4)_3HPO_4$ to provide the desired specific activity and the desired concentration of total P. The amount of additional P from the $H_3P^*O_4$ was less than 0.3 percent of the total P and was ignored in the computations for total P. Whenever a series of samples was counted, the pertinent series of four standard planchets was counted. These counts were used for plotting a calibration curve for the samples counted during any 2-hour period. This procedure insured the proper correction for decay of the P^{32} as well as for day to day variations in the counting instruments.

In contrast to the samples containing tagged phosphorus, those for determining total phosphorus were dissolved in 20 ml of 2N nitric acid for each ½ gm of dry tissue. To insure complete dissolution, the ash was allowed to stand for 2 days in the acid in a beaker covered with a piece of tightly fitting plastic film and stirred thoroughly before the aliquot was taken. Total phosphorus was determined colorimetrically on aliquots containing from 0.15 to 0.40 mg of P by the vanadate-molybdate method described by Richards (1954).

Determinations of total P on two samples of needles from the same container of seedlings had an average deviation from their mean of 3.9 percent. For determinations of P*, the precision was somewhat better with an average deviation within paired samples of only 2.5 percent of their mean.

Foliar Deposition of Phosphorus

To determine the amount of P which could be deposited on or in the needles of loblolly pine, the tops of 12 seedlings were cut from the roots and dipped immediately in the solution used for treatment IV which contained the tracer. In this experiment all of the needles were immersed. After the excess liquid had been drained from the surfaces of the needles, a sample was taken from each seedling and analyzed for P*.

In 1959 the amount of P* deposited was 5.60 mg per gram of ovendry needle tissue, with fiducial limits at the 5 percent level of ±0.62 mg. A similar result was obtained in 1960 when 5.9 mg of P* was deposited per gram of ovendried needle tissue. This is more than five times the normal sufficiency level for P in loblolly pine seedlings as determined by Fowells and Krauss (1959).

Translocation of Phosphorus

Translocation of P^{32} to the roots was observed in 1959 in a group of 48 seedlings to which tagged P was applied on about

half the foliage of each seedling. Three seedlings were harvested from this group at daily intervals during the first 6 days after treatment and on the 8th, 12th, and 16th days. Root tips were analyzed for P*.

Appreciable quantities of the translocated P* were detected in the root tips collected 24 hours after the foliar application. After 48 hours 0.39 mg of P* per gm of dry tissue was found in the root tips. This quantity, 18 percent of the total P present in those root tips at that time, was about as high as in any sample collected subsequently in this series. These results in general agree with those of Koontz and Biddulph (1957) who found that in bean leaves the rate of absorption decreased after 30 hours from the time of treatment.

In 1960, root tips collected 38 days after a foliar treatment contained 1.7 mg of P* per gm of dry tissue. This quantity is the portion apparently translocated from the foliar deposit and is about 75 percent of the total P present in the root tips at the time of sampling (2.3 mg of P per gm of dry tissue).

The amount of P translocated, expressed as a percentage of the total amount deposited on or in the foliage, was determined on seedlings grown in 1959. In the sample of 12 seedlings discussed in the preceding section, the mean amount deposited was 5.60 mg of P* per gram of ovendry needles, or 12.6 mg of P* deposited on each seedling. From the same population of seedlings, another sample consisting of 23 individuals was harvested 21 days after the foliar treatment. The seedlings were divided into needles and stem produced after treatment, the treated needles, the treated stems, and the roots. The amount of P* in each portion was determined.

From the new shoots produced during the 21 days following treatment, a mean of 0.76 mg of P* per seedling was recovered. The roots at the end of this period contained a mean of 0.30 mg of P* per seedling. The sum of these means, 1.06 mg, is a good estimate of the amount of P* translocated per seedling and was 8.2 percent of the amount deposited on or in the foliage at the time of treatment.

In the 1960 study, the seedlings grew after treatment for 5 weeks before samples were taken. Samples of the new growth consisted of needles only and contained 1.5 mg of P* per gram of dry tissue. This amount is 65 percent of the total P in these new needles. The total P was more than twice the sufficiency level observed by Fowells and Krauss (1959) for loblolly pine seedlings.

The uptake of P was much greater in seedlings supplied with P through their roots from a culture solution containing 50 ppm of P. Four weeks after this level of P was initiated, the amount of total P in mature needles increased from 1.3 mg to 3.3 mg per gm dry weight. In the needles on the new growth, the level was 4.6 mg per gm of dry tissue. Of this amount, 59 percent was taken up from the culture solution and 41 percent was translocated from other parts of the seedling. The total amount of phosphorus uptake indicates "luxury" consumption and therefore is not a reasonable standard for evaluating the efficiency of uptake from foliar applications.

The maximum non-injurious level of β radiation for loblolly pine seedlings under the conditions of this test was not known. To check on possible radiation effects, non-radioactive variants of treatments II and IV were included in the experiment. Differences between the radioactive and non-radioactive versions of these two treatments were determined for three criteria —total phosphorus content of the new needles formed after treatment, total dry weight, and height increment following treatment. These differences were not consistent among the four blocks and obviously not significant. The radiation levels used in this study, therefore, had no effect on the magnitude of the three factors which were measured.

Effect of Foliar Treatment on Growth

Height growth of seedlings receiving the foliage treatment was no greater than that

TABLE 4. Mean daily height growth following treatment.[1]

Treatment	Growth per day during first 22 days	Growth per day during next 14 days
	Inches	*Inches*
I. No P	.127	.040
II. P* thru roots	.189	----
III. P thru roots	.210	
IV. P* on foliage	.117	.097
V. P on foliage	.114	.112

[1] Measurements are means for 24 seedlings—4 crocks each containing 6 seedlings.

of seedlings receiving no P at all during the first 22 days after treatment (Table 4), but during the fourth and fifth week after treatment, the growth on seedlings receiving no P decreased to about half that for the foliarly treated seedlings.

Although the foliar treatment used in this test was better for growth than the treatment involving no additional P, there is apparently some inhibitory effect on growth because seedlings having 50 ppm of P available to their roots grew at almost twice the rate of seedlings with treated foliage. This inhibition is not attributable to lack of translocation, because abundant P was found in the shoot tips and root tips of foliarly treated seedlings. This suggests the need for further study with other combinations of concentration, pH, and surfactants.

Summary

The foliage of loblolly pine seedlings retained 5.6 mg of radioactivity tagged P (P*) per gram of ovendry needles after being immersed for less than 5 seconds in a 0.5 M solution of $(NH_4)_2HP^*O_4$ with 0.05 percent "Tween 20" added as a spreader. With this treatment, height growth of the seedlings was more than double that of seedlings receiving no P but was only 60 percent of that for seedlings with 50 ppm of P available to the roots.

An appreciable amount of the P* deposited on the needles was translocated to the root tips within 24 hours from the time of treatment. Maximum quantities of P* were found in root tips collected 48 hours after treatment.

Mean amount of P* per seedling deposited from the foliar immersion was 12.8 mg. Three weeks after treatment, 8.2 percent of this amount was recovered from the untreated portions of the seedling.

Five weeks after a foliar application of P* and with no P available to the roots during this period, needles collected from new shoots contained a total of 2.3 mg of P per gram of dry tissue. Of this amount, 65 percent was P* which had been translocated from the foliar deposit on the older needles.

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Principles of Plant Breeding

By R. W. Allard. John Wiley and Sons, Inc., New York. 485 pp., illus. 1960. $9.

Review by A. E. Squillace
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Breeding of agricultural crops, of course, began in earnest long before forest tree breeding. The work of agricultural crop breeders not only antedates that of forest tree breeders but is facilitated by the use of species having short reproductive cycles. In carrying on their effective endeavors agricultural crop breeders have tested many techniques, run into pitfalls in some instances, and have met with spectacular success in others. Needless to say, comparable workers in forestry can and should take advantage of their experience to the greatest extent possible.

"Principles of Plant Breeding," as the title implies, stresses the biological principles involved in plant breeding methods. The organization of the book may be somewhat confusing to some because of separation of material according to importance into two broad categories of plants: self-pollinated species and cross-pollinated species. For example, a basic discussion of quantitative inheritance is included under a section dealing with self-pollinated crops, while material dealing with population genetics is discussed in a section on cross-pollinated crops. But in spite of these objections, desired material can be found with comparative ease. Although an elementary knowledge of genetics is assumed of the reader, the text is easy to read. The author, of course, usually uses agricultural crops as examples but the stress on fundamentals makes it a valuable tool for breeders of all plant species.

The book is divided into sections, each containing several chapters. An introductory section discusses the nature and goals of plant breeding, patterns of evolution in cultivated species, plant introduction, reproductive systems, and finally outlines briefly the various plant breeding methods.

Section 2 covers the genetic basis of breeding self-pollinated crops, including chapters on principles of selection, genetic consequences of hybridization, quantitative inheritance, and related material.

Section 3 gives details of the various breeding methods applicable to self-pollinated crops. The treatment of quantitative genetics is lucid in many respects but, being slanted toward crop breeding, it does not cover all the heritability techniques available for application to forest tree breeding.

Section 4 then covers subjects basic to breeding of cross-pollinated crops, including a good discussion of the theory and consequences of selection and systems of mating. Inbreeding depression and heterosis are also well covered here, with a discussion of dominance and overdominance hypotheses of heterosis. The breeding methods with cross-pollinated crops then follow in Section 5. The presently popular recurrent selection method, which incidentally may have a counterpart in forest tree improvement, is discussed here.

Section 6 first rather thoroughly covers the variations in pathogenic capabilities of parasitic organisms and differences in disease resistance of the host plants and then outlines breeding programs designed to produce resistant varieties.

Section 7 delves into the inheritance and cytogenetics of polyploids, and the induction of polyploidy in plant breeding. Interspecific hybridization is covered in Section 8, and a final section includes two miscellaneous topics, mutation breeding, and the distribution and maintenance of improved varieties. Seed certification, which is presently of great interest to foresters, is treated under the latter topic. A short but valuable glossary is included.

An Index for Comparing Equations Used In Constructing Volume Tables

BY
GEORGE M. FURNIVAL

THE METHOD of least squares is now quite commonly used in the construction of volume tables. The popularity of the method is primarily due to its freedom from any subjective bias that may be involved in fitting a free-hand curve. However, the objectivity of the mathematical fit is somewhat clouded by the personal element that enters at the beginning with the choice of the volume equation.

This initial problem of choosing an appropriate form of equation can be extremely vexing. Large numbers of equations have been proposed for volume table construction and considerable difficulty may arise in attempting to decide which equation is most appropriate for a particular set of data. The usual index of fit, the root mean square residual, can be used to compare equations that have the same dependent variable but is not suitable when the dependent variables differ. Hence, for example, the mean square residual from Spurr's combined variable equation (Spurr 1952)

$$V = a + b\ D^2H \quad \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

cannot be compared to the mean square residual from the logarithmic equation of Schumacher and Hall (1933)

$$\log V = a + b \log D + c \log H \ldots\ldots (2)$$

where in both equations V is volume, D is diameter and H is height.

A further problem for the mensurationist in constructing volume tables may arise in the choice of a suitable set of discrete weights (Gedney and Johnson 1959) or of a suitable weighting function. Unweighted least squares estimates are fully efficient only when homoscedasticity exists or, in other words, only when the standard error of the residuals is constant for all classes of the dependent variables. Theoretically weights should be employed that are inversely proportional to the variance of the residuals but in practice it may be difficult to determine the most appropriate way to weight a particular equation.

For example, equation (1) is usually fitted with a weight of unity. But it is unlikely that the estimates so obtained use all the information available from the data. It has been noted (Kinashi and Schumacher 1958, Palley 1959, Gedney and Johnson 1959, Meyer 1953) that the standard error of the residuals from arithmetic volume equations tends to vary with the size of the trees. Large trees deviate more on the average from the regression surface than do small trees. It might be hypothesized that the standard error of the residuals is proportional to D^2H; the appropriate weight would then be $(D^2H)^{-2}$. Obviously, other hypotheses might also be made and other weights employed.

The question of weights as such can often be avoided by a simple transformation. Multiplying both sides of a volume equation by the square root of an appropriate weighting function will stabilize the standard error of the residuals; fitting the transformed equation with a constant weight will then be equivalent to fitting the untransformed equation with its vari-

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able weight. If equation (1) is to be fitted with a weight of $(D^2H)^{-2}$, for example, the sum of squares to be minimized is

$$\Sigma\,[(D^2H)^{-2}\,(V-a-bD^2H)^2]$$

$$\text{or } \Sigma\,(VD^{-2}H^{-1}-a\,D^{-2}H^{-1}-b)^2. \quad (3)$$

On the other hand, multiplying both sides of equation (1) by $(D^2H)^{-1}$ gives

$$VD^{-2}H^{-1} = b + a\,D^{-2}H^{-1} \quad \ldots\ldots (4)$$

If the standard error (S.E.) of the residuals from equation (1) is proportional to D^2H, then the standard error of the residuals from equation (4) is constant. For, if

$$\text{S. E. } (V - a - b\,D^2H) = k\,D^2H$$

then

$$\text{S. E. } (VD^{-2}H^{-1} - b - a\,D^{-2}H^{-1}) = k.$$

Furthermore the sum of squares to be minimized in fitting (4) with a constant weight is

$$\Sigma\,(VD^{-2}H^{-1} - b - a\,D^{-2}H^{-1})^2 \quad (5)$$

and, except for order, the two sums of squares, (3) and (5), are identical. Hence the regression coefficients obtained by fitting equation (1) with a weight of $(D^2H)^{-2}$ will be the same as those obtained by fitting (4) with a constant weight. Thus the choice between the two weights, unity and $(D^2H)^{-2}$, is equivalent to a choice between two equations, (1) and (4), each with a constant weight.

The reduction of the problem of weights and equations to one of equations alone presents no particular advantage unless some index of fit is available for comparing equations with different dependent variables. No such criterion has appeared in the literature but a solution to the problem can be obtained by employing the concept of likelihood.

All least squares estimates with unit weights are equivalent to maximum likelihood estimates under the assumption that the residuals are distributed normally, independently, and with a constant standard error (Johnson and Tetley 1950). Thus the values of the coefficients computed by least squares can be those that maximize the likelihood of the observed sample. It would appear reasonable, therefore, to go one step further and evaluate these maximum likelihoods for the equations under consideration. The computed likelihoods could then be used as a criterion for choosing the most appropriate form of equation. The requirement of independence, normality and a constant standard error may appear unduly restrictive but such is not the case. Other assumptions could be made about the distribution of the residuals but the set listed above enjoys the advantages of simplicity and utility. Independence of the residuals is a necessary condition for linearity; the existence of normality simplifies probability statements, and, as stated before, a constant standard error ensures efficient estimates of the regression coefficients.

The sets of residuals from a number of regression equations can not, in general, all be distributed normally, independently and with a constant standard error. If, for example, the residuals from equation (2) are distributed normally, then the residuals from equation (2) must follow a log normal distribution. Similarly, if the residuals from equation (4) have a constant standard error, then the residuals from equation (1) must have a standard error proportional to D^2H.

The magnitude of the likelihood computed for an equation will, however, be influenced by the failure of any one of the assumptions to hold for that particular equation. Furthermore the size of the residuals will also affect the value of the likelihood. Hence the use of likelihood as a criterion for choosing the most appropriate form of equation has the advantage of reflecting both the size of the residuals and possible departures from linearity, normality, and homoscedasticity.

The usual method of constructing likelihood functions is to form the logical product of the probability densities in the sample space of the dependent variable. Likelihood

functions constructed in this manner are comparable only in the same sample space, but fortunately probability densities in the sample space of some function, $f(V)$, of volume may be readily transformed to the sample space of volume by multiplying by the first derivative of the function.

For example, the probability density functions for equations (1), (2) and (4), respectively, are

$$P_1(V) = \sigma_1^{-1}(2\pi)^{-\frac{1}{2}} \exp -\frac{1}{2}\sigma_1^{-2}(V - a - b D^2H)^2 \quad \ldots\ldots(6)$$

$$P_2(\log V) = \sigma_2^{-1}(2\pi)^{-\frac{1}{2}} \exp -\frac{1}{2}\sigma_2^{-2}(\log V - a - b \log D - c \log H)^2 \quad \ldots\ldots(7)$$

$$P_4(VD^{-2}H^{-1}) = \sigma_4^{-1}(2\pi)^{-\frac{1}{2}} \exp -\frac{1}{2}\sigma_4^{-2}(VD^{-2}H^{-1} - b - a D^{-2}H^{-1})^2 \quad \ldots\ldots(8)$$

where the residuals from each equation in turn are assumed to be distributed normally, independently and with a constant standard error. The corresponding sample spaces, as indicated within the parentheses on the left, are volume, log volume and the ratio of volume to the product of diameter squared and height. Thus the derivatives necessary for transforming $P_2(\log V)$ and $P_4(VD^{-2}H^{-1})$ to the sample space of volume are

$$\frac{d(\log V)}{dV} = V^{-1}$$

$$\frac{d(VD^{-2}H^{-1})}{dV} = D^{-2}H^{-1}$$

On multiplying the right hand sides by the appropriate derivatives, equations (7) and (8) become

$$P_2(V) = V^{-1}\sigma_2^{-1}(2\pi)^{-\frac{1}{2}} \exp -\frac{1}{2}\sigma_2^{-2}(\log V - a - b \log D - c \log H)^2$$

$$P_4(V) = D^{-2}H^{-1}\sigma_4^{-1}(2\pi)^{-\frac{1}{2}} \exp -\frac{1}{2}\sigma_4^{-2}(VD^{-2}H^{-1} - b - a D^{-2}H^{-1})^2.$$

With all three probability density functions now in the same sample space, the likelihood functions may be formed from the logical products, as follows:

$$L_1(V) = \Pi P_1(V) = \sigma_1^{-n}(2\pi)^{-\frac{n}{2}} \exp -\frac{1}{2}\sigma_1^{-2}\Sigma(V - a - b D^2H)^2$$

$$L_2(V) = \Pi P_2(V) = [\Pi(V^{-1})]\sigma_2^{-n}(2\pi)^{-\frac{n}{2}} \exp \frac{1}{2}\sigma_2^{-2}\Sigma(\log V - a - b \log D - c \log H)^2$$

$$L_4(V) = \Pi P_4(V) = [\Pi(D^{-2}H^{-1})]\sigma_4^{-n}(2\pi)^{-\frac{n}{2}} \exp -\frac{1}{2}\sigma_4^{-2}\Sigma(VD^{-2}H^{-1} - b - a D^{-2}H^{-1})^2.$$

The likelihoods may be evaluated as they stand by substituting for σ^2 the estimate S^2, which is obtained by dividing the sum of squares of residuals by $n - r$ where n is the number of observations and r is the number of coefficients in the regression equation.

The calculated values may then be written as

$$L_1 = S_1^{-n}(2\pi)^{-\frac{n}{2}} \exp \frac{n}{2}$$

$$L_2 = [\Pi(V^{-1})]S_2^{-n}(2\pi)^{-\frac{n}{2}} \exp \frac{n}{2}$$

$$L_4 = [\Pi(D^{-2}H^{-1})]S_4^{-n}(2\pi)^{-\frac{n}{2}} \exp \frac{n}{2}$$

However further simplification is possible. Since relative rather than absolute values are of importance here, any monotonic functions of the likelihoods will serve. The

constant factor

$$(2\pi)^{-\frac{n}{2}} \quad \exp -\frac{n}{2}$$

may be dropped, *n-th* roots taken, and the results inverted to give

$$I_1 = S_1$$
$$I_2 = [V]\ S_2$$
$$I_4 = [D^2H]\ S_4$$

where the brackets now signify geometric means. The indices of fit (I) are, however, in inverse order as compared to the likelihoods; a large value indicates a poor fit and vice-versa.

The general equation for the suggested index of fit may be written as

$$I = [f'(V)]^{-1}S$$

where $f'(V)$ is the derivative of the dependent variable with respect to volume. The index reduces to the usual estimate of the standard error about the curve when the dependent variable is volume as in equation (1). When the dependent variable is some function of volume, the index may be regarded as an average standard error transformed to units of volume.

Computation of the Index

The computation of the suggested index of fit can best be described as a three-stage affair. First, root mean square residuals are obtained by fitting each equation to the data in turn. Next, the geometric means of the derivatives of the several dependent variables with respect to volume are computed with the aid of logarithms. Finally, each root mean square residual is multiplied by the inverse of the appropriate geometric mean.

For example, in testing equations (1), (2) and (4) on the data in the first three columns of Table 1, the initial step is to fit the equations by the usual method of least squares. The root mean square resi-

TABLE 1. Artificial data for constructing a volume table.

DBH (inches)	Merch. ht. (feet)	Volume (bd. ft.)	Log Volume	Log D^2H
14	16	78	1.8921	3.49636
14	20	85	1.9294	3.59329
14	14	67	1.8261	3.43838
14	16	71	1.8513	3.49638
16	32	170	2.2304	3.91339
16	24	124	2.0934	3.78845
16	20	115	2.0607	3.70927
18	36	215	2.3324	4.06685
18	40	274	2.4378	4.11261
20	48	300	2.4771	4.28330
Totals			21.1307	37.89830

TABLE 2. Computation of the index of fit.

Computations (symbolic)		Equation 1	Equation 2	Equation 4
S	(1)	19.15	.0323	.00152
$\Sigma \log [f'(V)]^{-1}$	(2)	0	21.1307	37.89830
$(2)/N$	(3)	0	2.1131	3.78983
antilog (3)	(4)	1	129.8	6164
(1) × (4)		19.2	4.2	9.4

duals obtained are 19.2, 0.303, and 0.00152 respectively.

The dependent variable of equation (1) is volume—alone and untransformed. Therefore the derivative involved is unity and the index of fit is simply the root mean square residual. The dependent variables of equations (2) and (4) are, however, the logarithm of volume and volume divided by D^2H. Hence the derivatives of the dependent variables with respect to volume are V^{-1} and $(D^2H)^{-1}$. The required geometric means can be obtained as the inverses of

$$\text{antilog} \frac{\Sigma \log V^{-1}}{n}$$

$$\text{and antilog} \frac{\Sigma \log (D^2H)^{-1}}{n}$$

or, more conveniently, the inverses may be obtained directly as

$$\text{antilog} \frac{\Sigma \log V}{n}$$

$$\text{and antilog} \frac{\Sigma \log (D^2H)}{n}$$

where n is again the number of observations.

The computations required for obtaining the indices of fit for equations (1), (2) and (4) are presented in Table 2. The index of fit for equation (2) is 4.2; for equation (4), 9.37; and for equation (1), 19.2. Thus it may be concluded that equation (2) is the most appropriate of the three for the data of this artificial example.

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Author's Correction

After the preceding article by George M. Furnival was in page proof an error in the calculations was detected. The derivative of log V should be $V^{-1} \log e$ throughout the text since common logs are used in the numerical calculations. The index for Equation (2) should therefore be $4.2(\log e)^{-1}$ or 9.7.

The Effect of Photoperiod on Growth, Photosynthesis, and Respiration of Loblolly Pine Seedlings From Two Geographic Sources

BY
WM. H. DAVIS MCGREGOR
ROBERT M. ALLEN
PAUL J. KRAMER

THE PHOTOPERIODIC response of various herbaceous species has been investigated intensively for many years and the literature has been reviewed by others. The effect of photoperiod on growth of woody species, and especially of forest tree species, has received much less attention, although Garner and Allard (1923) mention several woody species in their early studies. The present study was undertaken to investigate the effect of relative length of day and night on growth, photosynthesis, and respiration of loblolly pine (*Pinus taeda* L.) seedlings from two sources.

The literature relating to trees, reviewed by Gevorkiantz and Roe (1935), Wareing (1948, 1956), Downs and Borthwick (1956), and Kramer (1960), indicates that most woody species show photoperiodic sensitivity in initiation and cessation of growth, internodal extension, leaf abscission, cambial activity, and other processes. Races within species have been shown to vary in their photoperiodic response (Pauley and Perry 1954, Sylven 1940, Vaartaja 1954).

Studies with pines have shown responses similar to those of other woody species (Bogdanov 1931, Gustafson 1938, Jester and Kramer 1939, Langlet 1942-3, Wareing 1950, 1951, Vaartaja 1957). Loblolly pine has been studied in several of these investigations of photoperiodic responses. Loblolly pine seedlings grew in height all winter in a greenhouse under 14.5 hours of light and under continuous light, but they grew faster with continuous light (Kramer 1936). An 18-hour light period, in comparison with shorter periods, increased growth and induced premature initiation of spring growth (Phillips 1941). Kramer (1957) reported that an 8-hour photoperiod shortened the growing season and a 16-hour photoperiod prolonged it. An interrupted dark period has been found to have effects similar to those produced by a long period of continuous light. When a 14.5-hour dark period was interrupted by 0.5 hour of artificial light, loblolly pine seedlings grew twice as tall as seedlings which were under uninterrupted 14.5-hour dark periods. Growth began sooner and continued longer in the interrupted dark treatment (Zahner 1955).

The possibility that differences in photoperiod might cause differences in photosynthetic potential or efficiency and that this altered rate of photosynthesis might account in part for the increased growth under long day has received little attention. Wareing (1956) and Liverman (1955) proposed that a high-intensity "light" pro-

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cess and a "dark" process are involved in photoperiodic effects and that the light process may involve photosynthesis. Chinoy and Nanda (1951), working with one variety of wheat, found that net assimilation rates (increase in dry weight per plant), when calculated on a weekly basis, were highest for plants grown under long day and lowest for plants grown under short day. When assimilation rates per hour of illumination were compared, however, no differences were found. They concluded that the lesser dry matter production in short-day plants was due to lesser total quantity of carbohydrates produced in the reduced photoperiod and to greater loss in respiration, and not to lower photosynthetic efficiency of these plants. Watson (1956) found that there was some variation in photosynthetic efficiency, but that total photosynthetic surface was more strongly correlated with growth or yield.

In the present study, loblolly pine seedlings from two geographic seed sources were grown under long and short days for 2 months and the CO_2 exchange in photosynthesis and respiration was measured. The objective was to determine whether there were racial differences in growth, photosynthesis, and respiration, and whether exposure to the two different photoperiods affected these processes.

Experimental Material and Methods

Seed for trees used in the study was collected in the fall of 1954 from natural stands of loblolly pine in St. Johns County, Florida, and Floyd County, Georgia. The north-south separation of the two sources is about 300 miles and the altitudinal separation approximately 500 feet. Three important climatic factors are as follows:

Climatic factor	*Florida source*	*Georgia source*
Average annual precipitation (inches)	48	49
Average annual temperature (°F)	70	62
Average frost-free season (days)	309	207

Seedlings were grown in the Georgia Forestry Commission's nursery at Davisboro, Georgia, in 1955, and shipped to Durham, North Carolina, in December 1955. They were potted in 8-inch metal cans, and remained out-of-doors under normal-day length until April 17, 1956, when they were brought into the greenhouse and exposed to the experimental photoperiods. At this time, the seedlings had all broken dormancy and were making active height growth.

Seven seedlings of each source were subjected to each of two photoperiods in the greenhouse. A short day (9.5 hours) was maintained by a clock-controlled mechanism which brought a light-tight cover over the seedlings at 5:15 pm and removed it at 7:45 am each day. All light was natural daylight. A long day (15 hours) was provided by clock-controlled incandescent lights which provided 50 to 100 foot-candles each evening. The two groups of seedlings were placed close to each other, and differences in maximum and in minimum temperature between the two groups seldom exceeded 2°F. Minimum temperature was 64°F. Height of all seedlings was measured every 2 weeks.

Two months after treatments began, each seedling of randomly selected pairs was assigned at random to one of two matching plant chambers in a temperature control cabinet in the laboratory. This apparatus has been described in detail by Decker (1944). Temperature in the cabinet and chambers was maintained at 23 ±1°C, and 4000 ft.c. of light was provided in the chamber by a bank of 150- and 300-watt incandescent lamps over the water-shielded glass top of the outer cabinet. After 30 minutes of preconditioning in the outer chamber, each seedling was moved to the assigned plant chamber. With outside air circulating through the chambers, 20 minutes was allowed for photosynthesis to come to equilibrium.

After the equilibrium period, one chamber at a time was connected to a Grubb-Parsons infra-red gas analyzer and the

enclosed air was circulated through the system by a small pump. The carbon dioxide concentration was adjusted to 10 percent above or 10 percent below normal by injecting CO_2 into or absorbing CO_2 from the system for measurements of photosynthesis and respiration, respectively.

Apparent or net photosynthesis (CO_2 utilized in excess of that produced in respiration) was measured by recording the time required by each seedling to reduce the CO_2 concentration from 10 percent above to 10 percent below that of normal air. Measurements were alternated between the two chambers until three readings had been recorded for each seedling. After photosynthesis measurements were completed on all seedlings, two respiration measurements were made in the dark, recording the time required for a plant to increase CO_2 concentration from 10 percent below to 10 percent above that of normal air. Since the time intervals were inversely proportional to the rate of CO_2 utilization and production, and the volume of each closed system was known, the rates of apparent photosynthesis and of respiration could be calculated.

Total fascicle length was estimated for each seedling by first counting the number of fascicles within each flush of growth and then measuring the lengths of a sample of fascicles in each flush.

Results

Height growth. Seedlings under long day grew significantly (1-percent level) more than those under short day, both in absolute growth and in growth expressed as a percentage of initial height (Table 1). Analysis of variance showed no significant difference in growth of Florida seedlings as compared with Georgia seedlings, but there was a significant (5-percent level) interaction between source and photoperiod; the long-day treatment was more effective in stimulating height growth of Florida seedlings, which are subject to somewhat shorter days during the growing season in their locality of origin than are seedlings of the Georgia source. The greater effect was associated with a second flush of height growth on Florida long-day seedlings. This second flush was several centimeters long at the time the CO_2 exchange was measured. In all other source-photoperiod combinations only a single flush of height growth occurred.

Photosynthesis and respiration. Rates of photosynthesis and respiration were expressed as rates of CO_2 exchange per seedling, and per unit of fascicle length. The latter basis eliminated the effect of differences in total fascicle length among source-photoperiod combinations.

A comparison between sources showed

TABLE 1. Average height, height growth, growth percent, and total fascicle length of loblolly pine seedlings as affected by source and day-length treatment.

Source	Day length	Initial height[1]	Height growth	Relative growth[2]	Total fascicle length
	Hours	*Cm*	*Cm*	*Percent*	*Cm*
Florida	9.5	16.6	7.3	47.0	895
Georgia	9.5	21.7	10.0	46.7	1646
Average	9.5	19.2	8.6	46.9	1270
Florida	15.0	17.0	16.4	100.7	1276
Georgia	15.0	23.4	13.9	61.9	2074
Average	15.0	20.2	15.2	81.3	1675

[1]Height when photoperiod treatments were begun.

[2]Relative growth is expressed as a percent of initial height. Values in this column are average percents and cannot be calculated directly from the initial height and height growth values given in this table.

TABLE 2. Average rates of net photosynthesis (Ps) and respiration (Rs) in milligrams of CO_2 per seedling per hour as affected by seed source and day length.

	Short day		Long day		Average	
Source	Net Ps	Rs	Net Ps	Rs	Net Ps	Rs
Florida	22.0	3.5	34.7	4.4	28.4	3.9
Georgia	38.8	3.7	47.1	5.7	42.9	4.7
Average	30.4	3.6	40.9	5.0		

that, on a per seedling basis, Georgia seedlings carried on photosynthesis at a significantly higher rate than Florida seedlings (Table 2). However, when rates of photosynthesis per unit of fascicle length were compared it was shown that the differences in rates per seedling were caused by differences in amount of foliage, or total photosynthetic surface. An analysis of the relation between photosynthesis per plant and total fascicle length showed that photosynthesis was positively and significantly related to total fascicle length (Fig. 1). Differences in rates of photosynthesis between sources were not significant after the effect of fascicle length was accounted for (Table 3).

Photoperiod treatment differences (Table 2), although closely approaching significance, were not significant because of high variation among replicates. A larger sample would probably have demonstrated

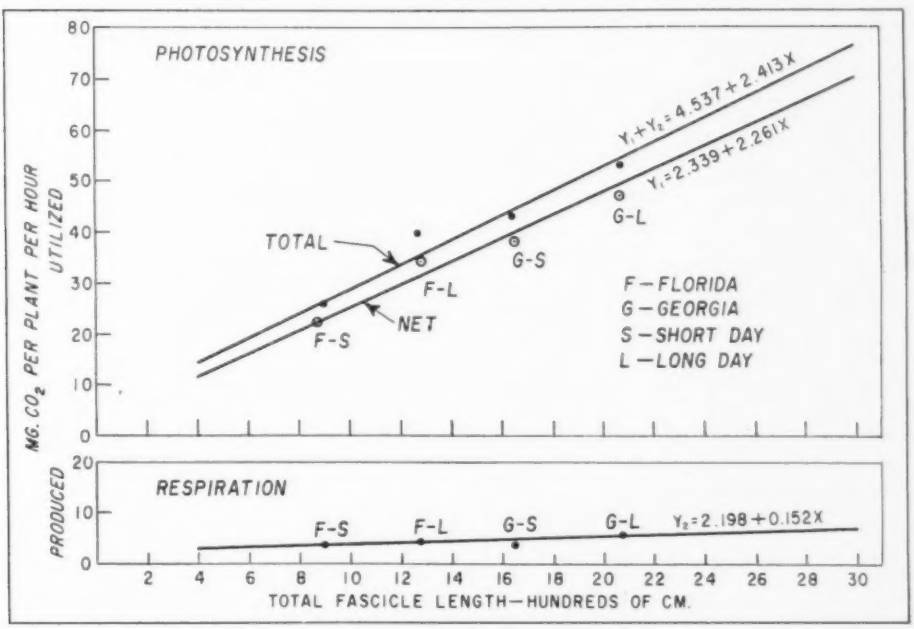

FIGURE 1. *Relationship between photosynthesis and respiration in milligrams of CO_2 per plant per hour and total fascicle length. Total photosynthesis as used here is the sum of net photosynthesis in the light and respiration in the dark. The points represent group averages.*

TABLE 3. Average rates of net photosynthesis (Ps) and respiration (Rs) in milligrams of CO_2 per 1000 cm of fascicle length per hour as affected by seed source and day length.

	Short day		Long day	
Source	Net Ps	Rs	Net Ps	Rs
Florida	24.5	3.9	27.2	3.9
Georgia	23.5	2.3	22.7	2.7

the statistical significance of this difference, since seedlings under long day were taller and had more foliage. When expressed as rate per unit of fascicle length, there were no differences between photoperiods (Table 3).

Respiration rates did not differ significantly between sources or photoperiod, whether expressed on the entire seedling or unit fascicle length basis. The regression of respiration per seedling on total fascicle length (Fig. 1) was not significant, but tends toward increased respiration with increasing amount of foliage. Logically this trend is real, because larger seedlings with more foliage could be expected to respire more. Respiration per unit of fascicle length tended to decrease and the Ps/Rs ratio correspondingly to increase with increasing amount of foliage per seedling.

Discussion

Since the rate of photosynthesis per seedling was found to increase with increasing amount of foliage, the widely used criterion of size for selection of outstanding seedlings in the nursery seems to have some sound physiological basis. Seedlings with larger tops and more needle area, carrying on photosynthesis at a higher rate than smaller seedlings of the same origin, should be capable of maintaining their size superiority. Increased mutual shading of needles may reduce the differences in rates of photosynthesis between large and small seedlings as the seedlings grow. Nevertheless, the larger seedlings, initially carrying on photosynthesis at a faster rate per seedling, should have a better chance of getting ahead of competing vegetation, provided they have enough roots to support the larger top and can survive the initial planting shock as well as the small seedlings.

The differences in rates of photosynthesis per seedling between sources and between photperiods appear to be accounted for by differences in amount of photosynthetic tissue as measured by total fascicle length. This suggests that at a given time in the season there are no differences in photosynthetic efficiency per unit of fascicle length within the species, even though there are considerable growth differences among individuals within the species according to sources and treatment. Chinoy and Nanda (1951) reached a similar conclusion. Huber and Polster (1955) found some clonal differences in rates of photosynthesis per unit of leaf area of poplars, but clonal differences in total leaf area caused much of the difference in rates of photosynthesis per plant. Watson (1956) also concluded that most treatments which increase yield or growth do so by increasing photosynthetic surface.

This raises the question of why total fascicle length is greater in some race-photoperiod combinations than in others. The greater total length of foliage of long-day seedlings might be a result of increased total daily photosynthate available because of the longer light period. However, the additional hours of light were a combination of early morning, late afternoon, and supplemental light, all of which are too low in intensity for appreciable photosynthesis (Daubenmire 1947). Apparently the effect of long photoperiod is to produce more potosynthetic tissue from a given amount of photosynthate This effect might be due to differences in efficiency of utilization of the total daily photosynthate, or to differences in the proportion of the utilized photosynthate which is diverted to growth of needles.

Likewise the differences in needle length which seem to account for racial or clinal differences in rates of photosynthesis per

seedling must be due to genetically controlled differences in either the efficiency of utilization of photosynthates or the apportioning of the utilized photosynthates among the various organs. These results support Kramer's (1957) conclusion that increased growth under long photoperiod resulted from more efficient utilization rather than from increased supply of food.

There appears to be some correlation between total photosynthesis per seedling and total height growth, largely because taller seedlings generally have more foliage. However, Florida seedlings under long day surpassed all other categories both in actual height increase and in growth as percent of initial height, although they did not have the highest rate of photosynthesis per seedling or the greatest amount of foliage. This again indicates that utilization of photosynthates varies between races and is affected by photoperiod.

Summary

1. One-year-old loblolly pine seedlings grown from seed originating in two geographic areas (Georgia and Florida) were grown under day lengths of 9.5 hours and 15 hours. Heights were measured every 2 weeks. After 2 months of treatment, the CO_2 exchange in photosynthesis and respiration was measured with an infra-red gas analyzer.

2. Absolute and relative growth of long-day seedlings was greater than that of short-day seedlings. Long-day treatment stimulated growth significantly more in Florida seedlings than in Georgia seedlings.

3. Georgia seedlings carried on photosynthesis at a higher rate than Florida seedlings but the difference in rates per seedling were caused by differences in amount of foliage, or total photosynthetic surface. Photoperiod had no significant effect on rate of respiration, either on a seedling or unit of fascicle length basis.

4. Long photoperiod apparently causes the production of more photosynthetic tissue from a given amount of photosynthate, rather than an alteration in the basic rate of photosynthesis. Racial or clinal differences in rate of photosynthesis per plant likewise appear to be due to differences in the amount of photosynthetic tissue produced from a given amount of photosynthate.

5. The difference in amount of photosynthetic tissue could be a result of differences in the efficiency of utilization of photosynthate or in the apportioning of the utilized photosynthates among the various organs.

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New Data on Distribution of Some True Firs of the Pacific Coast[1]

Note by Philip G. Haddock
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It is the purpose of this note to describe a little known occurrence of Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) in the Marble Mountains of Siskiyou County, California, and to correct an error in the reported occurrence of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.).

Roof (1959) credited the discovery of a stand of Pacific silver fir in the Marble Mountains of Siskiyou County, California to A. K. Crebbin, a forester on the staff of the Klamath National Forest at Yreka, California. Crebbin at the time was mapping native vegetation for the California vegetation type map survey. A. E. Wieslander,[2] then in charge of this mapping program for the U. S. Forest Service, became aware of Crebbin's discovery. Later he notified E. L. Little whose brief mention of it (Little 1953) and the description of Roof (1959) are the only references to the presence of the species in California noted in the literature. The writer has determined through personal correspondence with Crebbin[3] that these trees were first recognized as Pacific silver fir about 1932. Crebbin wrote in part as follows:

> I have found the species on two locations on the Klamath (National Forest); the first, near Hancock Lake in Sections 10, and 15, T. 41 N., R. 12. W., M.D.M. (Mount Diablo Meridian), and the other in the vicinity of Ukonum Lake in Section 22, T. 14 N., R. 7 E., H.M. (Humboldt Meridian). In both cases, the species is growing at an elevation above 6,000 feet on a cold north exposure.

The first location referred to by Crebbin is on the ridge between Wooley Creek and the north fork of the Salmon River, northwest of Sawyer's Bar, while the second is on the headwaters of Independence and Ukonum Creeks, tributaries which enter the Klamath River a few miles south of Happy Camp.

Roof (1959) reported that the wildlings of Pacific silver fir he transplanted to Tilden Park Botanical Garden were obtained in 1948 from the ridge between English Peak and Hancock Lake at an elevation of 7,000 feet through the courtesy of Assistant Supervisor A. K. Crebbin and District Ranger Andy Schmidt of the Klamath National Forest. The stand visited and described by Roof is accessible only by trail and lies within the Marble Mountain Wilderness Area on the ridge between Wooley Creek and the headwaters of the north fork of the Salmon River. The stand is described by Roof as follows:

> On the evening of our first day at 7,000 feet in the Marbles we determined that the fir stands in question were *Abies amabilis*. They are part of a most interesting square mile of the forest on the northern slopes of English Peak, in an area bounded by Hancock, English, Pine, and Diamond Lakes. Within the cold pocket of this square mile the balsam fir is found in several small pure groves, though it is mostly mixed with Shasta Fir, Weeping Spruce, Western White Pine, Mountain Hemlock, Brewer Oak and Sitka Alder, ... "Seedlings of *Abies amabilis* were plentiful along the trails, in the duff of the forest floor.

A check of standard reference books and other recent publications, Harlow and Harrar (1958), Munz and Keck (1959), Peck (1941), Schmidt (1957), and Dimock (1958), shows that this occurrence of Pacific silver fir in California is not generally known.

In December 1959, A. K. Crebbin very kindly sent the writer seeds of Pacific silver fir obtained by Ranger Groncki on September 21, 1959 from squirrel-cut cones in Section 10, T. 41 N., R. 12 W., (near Hancock Lake). As a check on the identification of the species and to verify the extension of range, these seeds were sown in the greenhouse at the University of British Columbia, Vancouver, along with sources of subalpine and Pacific silver fir seed obtained from stands native to

[1]The kind assistance of the following, in addition to those mentioned in the text, is acknowledged: Rimo Bacigalupi and the late G. Thomas Robbins, both of the Jepson Herbarium, Univ. of Calif., Berkeley, and John W. Duffield, Industrial Forestry Asso., Nisqually, Wash. Research Note No. 35, Faculty of Forestry, University of British Columbia. Manuscript received ept. 23, 1960.

[2]A. E. Wieslander, 79 Roble Road. Berkeley 5, Calif. Sept. 1960. Personal Correspondence and conversation.

[3]A. K. Crebbin, Klamath National Forest, Yreka, California, 31 July 1959. Personal correspondence.

British Columbia. Subsequent examination and comparison of the seedlings produced verifies the identification of the Siskiyou County, California source as Pacific silver fir.

In the summer of 1960 the writer observed the Pacific silver fir specimens collected in 1948 near Hancock Lake by Roof and transplanted to the Botanical Garden at Tilden Park; they were growing very well in their new home in the Berkeley Hills.

A species of Abies collected in 1928 from the "Salmon Mountains" at Hancock Lake in Siskiyou County, California was reported by Gillespie (1931) to be alpine (subalpine) fir. On the suspicion that this might have been mistaken for Pacific silver fir, the writer obtained Gillespie's specimen through the courtesy of the Dudley Herbarium of Stanford University. With the kind assistance of R. W. Kennedy and G. Ifju, of the Faculty of Forestry, University of British Columbia, needles from Gillespie's collection from Hancock Lake were embedded (dry) in "Epolene C" (an Eastman plastic), then sectioned with a sliding microtome and mounted in glycerin. From the criteria listed in Fulling (1934) and from other external morphological evidence it would appear that this specimen was misidentified and in reality is not *Abies lasiocarpa* (Hook.) Nutt.) but *Abies amabilis* (Dougl.).

It is important that natural occurrences of species be accurately determined and that corrections be made promptly. This is especially desirable when the species is an endemic or part of a relic stand which may contain genotypes potentially valuable for tree breeding. Heimburger and Holst (1955) conclude their paper with this sentence:

> A number of forest tree breeding problems are common to Canada and the United States, and the results of this trip should thus be of interest and value to forest tree breeders and forest geneticists in the northern, glaciated parts of the U.S. by pointing out possible sources of breeding materials in the unglaciated parts.

It is not to be inferred that the present site of Pacific silver fir in the Hancock Lake and Ukonum Lake areas was unglaciated during the most recent ice advance. On the contrary, small ice fields at least may have occupied the area. The "ancestors" of these trees probably grew at lower elevations in refugia along with various other species now found only at the higher elevations. It would be of interest to determine the nearest occurrence of Pacific silver fir to the north, since range maps show the southernmost station to be somewhere well north of the Oregon border. Peck (1941) stated that the species extends "from Crater Lake (north)". Sudworth (1908) gave the limits as "extreme southern headwaters of the Willamette River and Old Bailey Mountain (west side of Crater Lake)". Applegate (1939) stated that it is common on Old Bailey Mountain (west of Diamond Lake) and reaches the summit of the Umpqua-Rogue divide but does not occur on the Rogue River side. He did not find it in Crater Lake National Park nor did Bailey and Bailey (1941) report it from there. Brown[4] concurs in Bailey and Bailey's (1941) opinion that neither noble nor Pacific silver fir appear to be present in Crater Lake National Park.

The stands of Pacific silver fir now growing in the Hancock and Ukonum Lake areas of Siskiyou County, California should be protected, if necessary by special measures. They would appear to be in no immediate danger, at least from loss by cutting, since the areas are both within the limits of the Marble Mountain Wilderness Area of the Klamath National Forest. Nevertheless, since this and other species of *Abies* are especially vulnerable to fire loss (Schmidt 1957), these isolated provenances should be preserved by cultivation in arboreta where they would be available to forest geneticists and tree breeders.

[4]Richard M. Brown. Assistant Park Naturalist, Crater Lake National Park, Oregon, Aug. 31, 1960. Personal correspondence.

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Forest Entomology

By T. O. Thatcher. Burgess Publishing Co., Minneapolis, Minn. 225 pp. $4.50.

Review by W. L. Baker
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The author offers this textbook as a practical approach to teaching the forestry aspects of entomology to students who intend to become professional foresters.

The first half of the book includes chapters on history, insect structure, insect development, ecology, and taxonomy. More than is usually the case, the author succeeded in bringing these subjects alive. These chapters are excellently done; the one on ecology especially. The chapter on taxonomy, a subject requiring more than ordinary skill in presentation, should prove useful to the practicing forester—it is simple enough in construction to be handled without too much trouble, and the terminology is not very difficult to understand.

The second half of the book includes chapters on economics, general control, biological control, cultural control, chemical control, application of control, and example life histories of forest insects. The chapters on economics and control are fairly comprehensive but suffer from not always being up-to-date. The same can be said of the discussions of insect-caused losses. The latter section must have been prepared before the Forest Service issued Timber Resources Review several years ago. Some of the control practices discussed are no longer recommended. The section on forest insect surveys is weak—it contains no mention of biological evaluations. Biological control is a broader subject than the author leads one to believe. Discussion of this subject is far from being up-to-date or complete.

It is unfortunate that this book sticks so closely to conditions in the Rocky Mountains. This may detract from its appeal to many readers. It is also unfortunate that the author reverted so often to the subjective approach in many of his discussions. This seems out of place in a textbook. However, these faults—if faults they be—are not particularly serious. Generally speaking, this is an excellent textbook, and it is recommended reading for anyone interested in forest entomology, as well as for forestry students.

Field Identification of Roots of Conifers in the Inland Empire

BY
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C. D. LEAPHART
F. D. JOHNSON

DURING the course of investigations of root systems of western white pine (*Pinus monticola* Dougl.) and its associated species in the Inland Empire,[1] sampling methods have been developed which require accurate identification in the field of large numbers of roots—particularly the small rootlets (Leaphart 1958)[2]. Because no information on field identification of coniferous roots is available, the key for field identification and the descriptions presented in this paper have been developed. Identification of roots larger than 2 mm in diameter is facilitated through the use of the field key and descriptions given here. Positive field identification of smaller roots cannot be assured, as the characteristics used here for differentiation are often poorly developed in such roots.

The diagnostic characteristics utilized in this paper are limited to those macroscopic features that can be observed with the naked eye or by use of a 10× hand lens. Microscopic features provide an excellent basis for laboratory identification of coniferous roots (Noelle 1910),[3] but are impractical for quick and accurate field identification.

The 11 most important commercial tree species (all conifers) of the Inland Empire are included in the key and their root characteristics described. Since some of these species rarely occur together in the same natural habitat, the problem of field identification is usually restricted to fewer than 11 species. Roots of herbs, shrubs, and a few broadleaf tree species are frequently encountered in sampling for conifer roots, but because of the absence of resin ducts and because of distinctive differences in color and texture, they do not complicate the identification. When conifers not included in the key are present in sampling areas, their roots should be examined first to avoid inaccurate identification of other roots.

Although no references to the field identification of roots of forest tree species have been found in the literature, a number of papers on general bark structure and identification are available. Among the most useful is the work of Chang (1954)[4] on bark structure of North American conifers. This work, however, deals exclusively

[1] The Inland Empire refers to Idaho north of the Salmon River and the adjacent forested areas of eastern Washington, western Montana, and southern British Columbia.

[2] Leaphart, Charles D. Root characteristics of western white pine and associated species in a stand affected by pole blight of white pine. Intermtn. For. and Rge. Expt. Sta. Res. Paper 52, 10 pp. 1958.

[3] Noelle, W. Studien zur Vergleichenden Anatomie und Morphologie der Koniferenwurzeln mit Rüchsicht auf die Systematik. Bot. Zeitung 68:169-266. 1910.

[4] Chang, Ying-pe. Bark structure of North American conifers. U. S. Dept. Agric. Tech. Bull. 1095, 86 pp. 1954.

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with bark on large stems, and gives no information on structure of the bark of roots. The terms "outer bark" and "inner bark" as used in this paper are based on Chang's definitions.

Roots of the same species growing under different environmental conditions show considerable variation in gross morphology. Consequently, all of the variation encountered cannot be considered in the key to the species, and only the most reliable characters have been employed in its construction. The discussions following each description have been designed to point out this variation.

The following species are treated in this paper:

Abies grandis (Dougl.) Lindl. (grand fir)
Abies lasiocarpa (Hook.) Nutt. (subalpine fir)
Larix occidentalis Nutt. (western larch)
Picea engelmannii Parry (Engelmann spruce)
Pinus albicaulis Engelm. (whitebark pine)
Pinus contorta Dougl. (lodgepole pine)
Pinus monticola Dougl. (western white pine)
Pinus ponderosa Laws. (ponderosa pine)
Pseudotsuga menziesii var. *glauca* (Beissn.) Franco (Rocky Mountain Douglas-fir)
Thuja plicata Donn. (western redcedar)
Tsuga heterophylla (Raf.) Sarg. (western hemlock)

A major division of the species into two groups is based on the texture of the dead outer bark. Roots of Rocky Mountain Douglas-fir, Engelmann spruce, the pines, and western larch are characterized by a conspicuously scaly outer bark with broad linear to platelike scales. The true firs, western hemlock, and western redcedar, on the other hand, have roots with the outer bark smooth or made up of narrow shredlike scales. Characters used to separate species within these two major groups include: color of the living inner bark, taste, color changes on exposure, distinctness of annual rings in the wood, resin canals in the wood, striations on the cambial surface of the wood, mucilaginous bark, resin pockets in the bark, and markings on the cambial surface of the inner bark.

FIELD KEY TO ROOTS OF INLAND EMPIRE CONIFERS

1a. Outer bark conspicuously scaly with broad linear to platelike scales; resin ducts present in wood.
  2a. Annual rings in the wood indistinct.
    3a. Inner bark bright to dull red immediately under the scaly outer bark; taste extremely bitter.
      4a. Reddish layer superficial, easily rubbed off with finger; wood and bark surfaces in cambial region not becoming yellowish.
        1. *Larix occidentalis*
      4b. Reddish layer not easily rubbed off with finger; wood and bark surfaces in cambial region rapidly becoming yellowish on exposure to air.
        2. *Pseudotsuga menziesii* var. *glauca*
    3b. Inner bark flesh-colored; taste mildly resinous to bitter.
      5a. Whitish striations on wood surface conspicuous; resin ducts conspicuous in cross sections; inner bark remaining pale flesh-colored on exposure.
        6a. resin pockets conspicuous in bark.
          3. *Pinus albicaulis*
        6b. Resin pockets inconspicuous or apparently absent in bark.
          4. *Pinus monticola*
      5b. Whitish striations on wood surface inconspicuous or absent; resin ducts inconspicuous in cross sections; inner bark becoming pale purplish on exposure.
        5. *Picea engelmannii*
  2b. Annual rings in wood distinct.
    7a. Taste of inner bark distinctly anise-like; roots usually contorted with an angular appearance.
      6. *Pinus contorta*

7b. Taste of inner bark like orange peel; roots usually not contorted.

7. *Pinus ponderosa*

1b. Outer bark smooth or with narrow shred-like scales; resin ducts not present in wood.

8a. Bark mucilaginous, with streamers of viscous liquid forming between torn edges of bark; inner mark generally thick and reddish-purple to the cambium.

9a. Resin pockets conspicuous in bark.

8. *Abies lasiocarpa*

9b. Resin pockets inconspicuous or apparently absent in bark.

9. *Abies grandis*

8b. Bark not mucilaginous; bark layer whitish next to the cambium.

10a. Outer bark fibrous; inner bark thin with extremely thin reddish layer; inner surface of bark not speckled.

10. *Thuja plicata*

10b. Outer bark not fibrous; inner bark thick with reddish layer often extending deep into inner bark layer; inner surface of bark speckled with small, purplish, lenticular markings.

11. *Tsuga heterophylla*

1. *Larix occidentalis* Nutt. (western larch)

Outer bark dark gray- brown to almost black or reddish-brown, made up of thin, linear, overlapping scales, easily separated from inner bark; outer bark thin.

Inner bark light purplish-red to reddish-brown or bright red immediately beneath the outer bark; reddish layer very thin, easily rubbed off to expose the yellowish or cream-colored bark tissue beneath; longitudinally cut surfaces of inner bark often showing fine irregular whitish to yellowish striations or blotches; resin pockets not visible to the naked eye; total thickness of inner bark about two-thirds of the total bark thickness.

Wood with inconspicuous resin ducts visible with hand lens but not apparent to the naked eye; annual rings inconspicuous.

Taste very bitter; odor mild, not distinctive.

Roots of western larch are sometimes very difficult to distinguish from those of Douglas-fir. Both have the reddish layer immediately beneath the outer bark and are very bitter in taste. The ease with which the superficial reddish layer in larch roots may be rubbed away usually enables one to make the distinction. In some small roots the reddish coloration may be poorly developed. The yellowish discoloration of the freshly exposed cambial surfaces of Douglas-fir roots is a helpful basis for identification in these cases.

2. *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco (Rocky Mountain Douglas-fir)

Outer bark dark reddish-brown to light brown, scales mostly linear, tending to overlap, usually rather sinuous, paler on under side; outer bark thin in relation to inner bark.

Inner bark light-reddish to flesh-colored immediately under outer bark; reddish coloration superficial or extending deep into the inner bark, not easily rubbed away; freshly exposed cambial surfaces rapidly becoming yellowish; longitudinally cut surfaces of inner bark often with fine whitish striations; resin pockets not visible to naked eye; inner bark thick in comparison to outer bark.

Wood with inconspicuous resin ducts visible with hand lens; annual rings not conspicuous; cambial surface rapidly becoming yellowish on exposure.
posure.

Taste very bitter; odor mild, slightly resinous.

As pointed out previously, Douglas-fir roots are very similar to those of western larch. Because these two species often occur together, differentiation is most troublesome for the root investigator. The diagnostic features for separation of the two species are discussed under western larch.

3. *Pinus albicaulis* Engelm. (whitebark pine)

Outer bark pale brownish; scales rather linear, loosely overlapped in several layers; outer bark very thin.

Inner bark pale carrot-colored to pinkish or pale reddish beneath outer bark; color superficial, whitish below to the cambium; longitudinally cut surfaces of inner bark with conspicuous whitish striations; resin pockets conspicuous to naked eye.

Wood with distinct resin ducts visible to the naked eye on both transverse and longitudinal sections; annual rings inconspicuous; rays conspicuous; whitish longitudinal striations conspicuous on cambial surface.

Taste and odor carrot-like.

The roots are very similar to those of western white pine. One feature, the presence of conspicuous resin pockets in the bark, provides a reliable diagnostic feature.

4. *Pinus monticola Dougl.* (western white pine)

Outer bark scales light grayish-brown, buff, or darker brown; scales rather linear, up to 7 mm wide, very thin, generally well developed even on very small roots; outer bark very thin; scars of old rootlet attachments often visible on outer surface.

Inner bark pinkish flesh-colored immediately beneath outer bark, most of inner bark whitish to flesh-colored, slowly becoming brownish after exposure; resin pockets not visible; inner bark very thick in relation to outer bark.

Wood with conspicuous resin ducts easily visible to the naked eye in transverse or longitudinal sections; annual rings not conspicuous; rays visible without hand lens; cambial surfaces with conspicuous whitish longitudinal striations.

Taste sharply astringent, momentarily puckers up mouth; odor sweetish, carrot-like.

Roots of western white pine can usually be distinguished from those of associated species by the pale, flesh color of the inner bark and the conspicuous white longitudinal striations on the cambial surface of the wood. The astringent taste is also a generally reliable character. Roots in general are rarely branched and with a noticeably sparse development of a fibrous root system. Engelmann spruce roots are similar but lack the conspicuous whitish striations on the wood, have a distinctly different bitter taste, and also differ in that the inner bark becomes a pale purplish on exposure.

5. *Picea engelmannii* Parry (Engelmann spruce)

Outer bark similar to that of western white pine but generally chestnut to dark brown; scales broad, linear, tending to overlap more than those of western white pine; relatively thin in relation to entire bark layer.

Inner bark pale flesh-colored, slowly changing to purplish-brown on exposure to air; making up most of bark layer and almost white next to cambium; resin pockets absent.

Wood with two conspicuous resin ducts in primary xylem of small roots, others inconspicuous; annual rings not conspicuous; whitish striations not present on wood surface.

Taste bitter but unlike that of western white pine.

The similarity of roots of Engelmann spruce and western white pine has been previously discussed under the description for the latter species.

6. *Pinus contorta* Dougl. (lodgepole pine)

Outer bark reddish-brown to light cinnamon or grayish-brown; scales linear to very broad, often encircling entire root, very thin and papery; outer bark layer very thin.

Inner bark thick, making up most of bark layer, pale pinkish to brownish-red next to outer bark; whitish next to cambium and through most of inner bark layer; resin pockets not apparent.

Wood with inconspicuous resin ducts that are visible with a hand lens; annual rings generally conspicuous; faint whitish longitudinal striations sometimes present on cambial surface.

Taste distinctly anise-like, slowly becoming astringent with a slightly bitter aftertaste; odor faintly anise-like.

Lodgepole pine roots frequently have an angular contorted appearance that has not been observed in the other species under study. The distinct anise-like taste helps distinguish the roots of this species from those of ponderosa pine, with which they are most likely to be confused.

7. *Pinus ponderosa* Laws. (ponderosa pine)

Outer bark light chestnut brown on older roots to tan on younger roots; scales prominent, linear, frequently overlapped, thin; outer bark layer very thin.

Inner bark flesh-colored to reddish-brown in some areas on outer surface; resin pockets not visible; inner bark makes up most of total bark layer.

Wood with inconspicuous resin ducts

visible with hand lens; annual rings usually visible to naked eye.

Taste like orange peel; odor faintly fragrant.

Ponderosa pine roots are similar to those of lodgepole pine but lack the distinct anise-like taste of the latter. The lack of striations on the cambial surface of the wood and the absence of a purplish color of the inner bark on exposure to air distinguish ponderosa pine roots from those of western white pine and Engelmann spruce.

8. *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir)

Outer bark dark brown to blackish-red; with thin, narrow shreds that often give an overall shaggy appearance to the roots; thin in relation to thick layer of inner bark.

Inner bark purplish-red with coloration extending almost to cambial region; very mucilaginous, with streamers of viscous liquid forming between torn edges of bark; resin pockets abundant and conspicuous to the naked eye; cambial surface of inner bark lighter in color with small darker blotches; entire inner bark layer very thick in relation to outer bark.

Wood with inconspicuous annual rings; resin ducts absent; usually with a small reddish pith in the center of transverse sections.

Taste and odor not pronounced; bark becoming very pulpy and mucilaginous when chewed.

Subalpine fir and grand fir roots are characterized by their thick bark, the shredlike scales of the outer bark, and the mucilaginous nature of the bark. Roots of the two species may be differentiated by the conspicuous resin pockets in the bark of subalpine fir.

9. *Abies grandis* (Dougl.) Lindl. (grand fir)

Outer bark orange on young roots to dark purplish-brown on older ones; smooth or with thin shreds giving surface a rippled appearance; extremely thin.

Inner bark very thick, comprising most of bark layer; pale orange-red to purplish-red and uniform nearly to cambium; inner surface cream-colored and faintly speckled; mucilaginous as in subalpine fir; resin pockets inconspicuous.

Wood with resin ducts absent; annual rings not conspicuous, but visible with hand lens; whitish striations on wood surface.

Taste mild; odor mild.

Roots are generally profusely branched with a very well-developed fibrous root system. Scars of old rootlet attachments are fairly conspicuous. Grand fir roots are very similar to those of subalpine fir, as discussed under the description for the latter.

10. *Thuja plicata* Donn. (western redcedar)

Outer bark light to dark brown; fibrous or shreddy; extremely thin.

Inner bark pinkish to purplish-red immediately below outer bark; rest of inner bark white, comprising most of bark layer; resin pockets absent.

Wood with no resin ducts; annual rings faintly visible; prominent red pith present.

Taste mild; odor not evident.

Roots can usually be readily recognized because of their extremely thin outer bark with a thin pink to purplish layer immediately beneath. However, very young red cedar roots may have a thick white pulpy outer layer with a thin pink layer next to the very small cylinder of wood. The root system is generally extensively branched with profuse development of absorbing rootlets.

11. *Tsuga heterophylla* (Raf.) Sarg. (western hemlock)

Outer bark light reddish-brown to dark reddish-purple (almost black); smooth to rippled; thin.

Inner bark relatively thick, making up most of bark layer; orange to purplish-red grading to white on inner surface; inner surface conspicuously speckled with small purple lenticular flecks parallel to wood grain; resin pockets absent.

Wood without resin ducts; annual rings not prominent to naked eye.

Taste extremely bitter.

Roots of western hemlock may be difficult to distinguish from grand fir roots on the basis of external appearance alone. However, they can be separated on the basis of taste as grand fir roots are not bitter and their bark is mucilaginous and becomes slimy with chewing. The fibrous root system of western hemlock is generally quite well-developed.

Shoot Elongation Characteristics of Forest Trees

BY
THEODORE T. KOZLOWSKI
RICHARD C. WARD

IT IS WELL KNOWN that different parts of trees grow at varying rates and at different times (Kramer and Kozlowski 1960). Diameter growth of stems and elongation of roots usually are characterized in the literature as more sensitive than height growth to variations in environmental factors. Seasonal height growth curves vary much less from year to year than do curves of diameter growth. In general, height growth has been represented as a continuous process which can be characterized by a rather smooth sigmoid curve. Such growth curves, which usually are based on averaged observations taken on a number of trees, do not characterize the growth patterns of individual trees. This paper reports a study of seasonal height growth patterns of individual trees of several species of gymnosperms and angiosperms under conditions of intense competition as well as in the absence of competition. It also deals with variations in shoot elongation on different parts of trees.

Methods

Seasonal height growth of ten randomly selected trees of each of five species of coniferous trees and nine species of deciduous trees was studied in central Massachusetts during the growing season of 1954. At the beginning of the experiment, the conifers were three-year-old seedlings grown under regular nursery management at the State Forest Nursery, Amherst, Mass. The soil was Melrose fine sandy loam with a moisture equivalent of 16.16 percent and a permanent wilting percentage of 5.52 percent. The deciduous trees varied in age from two to ten years, but all individuals of the same species were of the same age. The hardwoods were widely spaced for maximum development and were growing in a soil of high fertility under regular nursery management at Adams Nursery, Westfield, Massachusetts. The soil was Chicopee fine sandy loam with a moisture equivalent of 6.83 percent and a permanent wilting percentage of 2.45 percent.

The terminal shoot of each of ten randomly selected trees of each species was measured for increase in height at approximately weekly intervals from early April until height growth was completed. The coniferous species used were white spruce (*Picea glauca* (Moench) Voss), Norway Spruce (*Picea abies* (L.) Karst.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), red pine (*Pinus resinosa* Ait.), and balsam fir (*Abies balsamea* (L.) Mill.). The deciduous species used were sugar maple (*Acer saccharum* Marsh), silver maple (*Acer saccharinum* L.), Kentucky coffeetree (*Gymnocladus dioicus* (L.) K. Koch), mountain-ash (*Sorbus americana* (Marsh.) DC.), paper birch (*Betula papyrifera* Marsh.), witch hazel (*Hamamelis virginia* L.), flowering dogwood (*Cornus florida* L.), sourwood (*Oxydendrum ar-*

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borcum (L.) DC.) and horsechestnut (*Aesculus hippocastanum* L.).

For an additional evaluation of height growth of different species on the same site and of variations in amount of shoot growth on different parts of the same tree, observations were taken on eight red pine, eight white pine, ten white spruce and ten black spruce (*Picea mariana* (Mill.)B.S.P.) trees. Different numbers of trees were used because of the variations in numbers of branches. The trees had completed six years of growth in a plantation on Plainfield sand at Wisconsin Rapids, Wisconsin. Spacing was approximately three by three feet.

In red pine and white pine, growth of the terminal leader for the 1960 season was measured on July 11, 1960 after shoot growth was completed. Shoot elongation for 1960 was also measured for all branches of the first (terminal) whorl and the second, third, and fourth whorls from the apex. Thus, 1960 growth of primary and secondary axes was measured in the terminal whorl; secondary and tertiary axes in the second whorl; and secondary, tertiary, and quaternary axes in the third and fourth whorls. Both the third and fourth whorls contained two sets of tertiary axis shoots, one set emanating just below the branch terminal bud (upper set) and the other set located along the branch at some distance from the main tip (lower set). In white spruce and black spruce, measurements were confined to 1960 growth of the primary axis (terminal leader) and secondary axes of the first (terminal), second, third and fourth whorls of branches.

Shoot growth data for primary axes are based on eight observations each for white pine and red pine, and ten observations each for white spruce and black spruce. Growth data for secondary axes are based on approximately equal numbers of randomly selected shoots from each tree in each species. For secondary axes at each stem position the number of observations varied from 32 to 40 depending on the number of axes available. All observations on tertiary and quaternary axes are based on 40 measurements per axis for each whorl and stem position. Approximately equal numbers of observations were taken on each tree.

Results

Amount of height growth. The total amount of height growth in the Massachusetts nursery of each coniferous seedling is given for each month in Figure 1. In some species growth varied greatly among individual trees while in other species the variation among individuals was less. For example, growth of individual seedlings of Norway spruce varied greatly and one seedling made about six times as much growth as another seedling. However, the variations among individual seedlings of hemlock and balsam fir were much smaller. Large variations in leader elongation between and within species are also shown in Table 1.

Seasonal distribution of height growth. As may be seen in Figure 2 there often are variations in seasonal distribution of growth among individual seedlings of the same species. Some Norway spruce seedlings made most of their growth in May while others made most growth in June and all seedlings had virtually completed their growth by the end of July. In contrast, three out of ten white spruce seedlings showed a secondary burst of growth in July and August after considerable growth in May but only negligible growth in June. Five balsam fir seedlings grew more in May than in any other month but five other seedlings made the most growth in June. The majority of the eastern hemlock seedlings made most of their growth in June and growth declined rapidly thereafter. Nevertheless, four of the seedlings grew approximately as much in July or August as in June. One eastern hemlock seedling grew more in August than in any other month. Although various red pine seedlings showed differences in amounts of growth they differed little in the seasonal distribu-

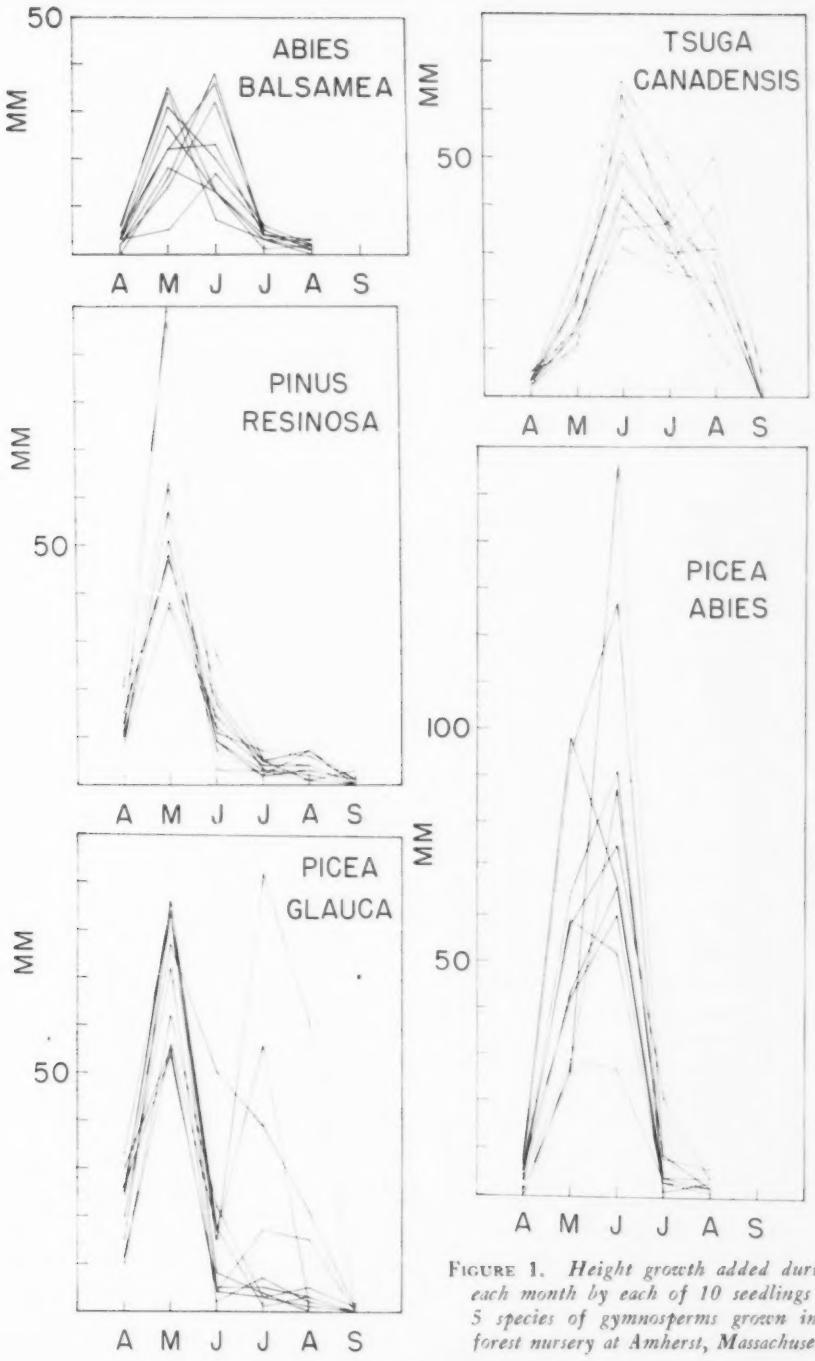


FIGURE 1. *Height growth added during each month by each of 10 seedlings of 5 species of gymnosperms grown in a forest nursery at Amherst, Massachusetts.*

TABLE 1. Variations in shoot elongation during 1960 on different locations of stems of 6-year-old conifers grown at Wisconsin Rapids, Wisconsin. All measurements are in centimeters.

	Primary axis	Secondary axis Whorl number				Tertiary axis Whorl number					Quaternary axis whorl number	
	(Terminal leader)	1 (Terminal)	2	3	4	2	3 Upper set	3 Lower set	4 Upper set	4 Lower set	3	4
Red pine	57.7 ± 6.2	34.6 ± 7.7	32.5 ± 4.9	27.7 ± 5.4	15.4 ± 8.0	17.1 ± 5.8	15.3 ± 5.4	13.7 ± 4.5	11.5 ± 4.9	8.1 ±4.8	6.2 ±2.7	4.7 ±2.5
White pine	44.3 ± 7.6	25.5 ± 8.2	24.8 ± 7.0	19.1 ± 4.1	14.1 ± 2.2	12.3 ± 5.1	10.5 ± 3.4	9.5 ± 3.4	7.8 ± 8.4	7.3 ±3.7	4.3 ±0.6	3.0 ±0.5
White spruce	33.5 ± 5.7	19.8 ± 4.1	17.4 ± 3.5	15.3 ± 2.8	11.8 ± 3.0							
Black Spruce	23.8 ± 6.4	17.3 ± 3.5	16.5 ± 2.5	14.1 ± 3.3	10.0 ± 3.2							

tion of their growth. All red pine seedlings made a rapid early-season spurt of height growth with a maximum in May and a consistent decline thereafter.

Figure 2 shows the cumulative percentages of height growth of each coniferous and deciduous seedling that had been completed at various dates during the growing season. Some pronounced species characteristics are evident such as generally short, long, or intermediate growing seasons for all seedlings of a particular species. However, of equal interest is the degree of variation in growth patterns among individual trees within species. The growth pattern of individual trees for species such as red pine and mountain-ash varied very little while eastern hemlock and Kentucky coffeetree showed somewhat greater variations. But, in contrast, very large variations in seasonal growth pattern occurred among individual trees of dogwood, paper birch, horsechestnut, witch hazel, sourwood, balsam fir, and white spruce. The large variation in growth among individual dogwood trees is indicated by the observation that on June 19 one tree had completed only 22 percent of its seasonal growth while another tree had completed 88 percent. There also was variation in consistency of bud bursting among species. Whereas bud break of all dogwood trees occurred at about the same time, there was a difference of approximately seven weeks from the time of bud burst of the first and last horsechestnut tree.

There were also variations among individuals in rates of growth. Some individual trees showed increase in growth at each date of measurement while others grew for a while, stopped, and then grew again. In balsam fir, horsechestnut, and eastern hemlock several trees demonstrated variations in rates of growth during the growing season.

Shoot elongation on different parts of trees. As may be seen in Table 1 large variations occurred in the amount of annual shoot growth of different species and on different parts of the tree within a species. In general, total growth of primary axes and secondary axes was in the following order: red pine>white pine>white spruce >black spruce. In addition, all species showed strong correlative growth inhibition. The primary axis grew more than a secondary axis; a secondary axis grew more than a tertiary axis; and a tertiary axis grew more than a quaternary axis. Also growth of the secondary axis was greatest at the terminal whorl and decreased progressively down the tree in the

second, third and fourth whorls. Similarly shoot growth of the tertiary and quaternary axes decreased from the top toward the bottom of the tree. When two sets of the same axis occurred on the same branch, as in the case of tertiary axes on the third and fourth whorls, the tertiary axis closer to the branch tip (upper set) grew more than the tertiary axis located at a greater distance from the tip (lower set).

Discussion

Shoot growth of trees is a highly variable and intermittent process. As shown in the present study both the amount and seasonal distribution of height growth vary greatly between species and often between individual trees of the same species. The amount of annual shoot elongation also varies greatly on different parts of the same tree.

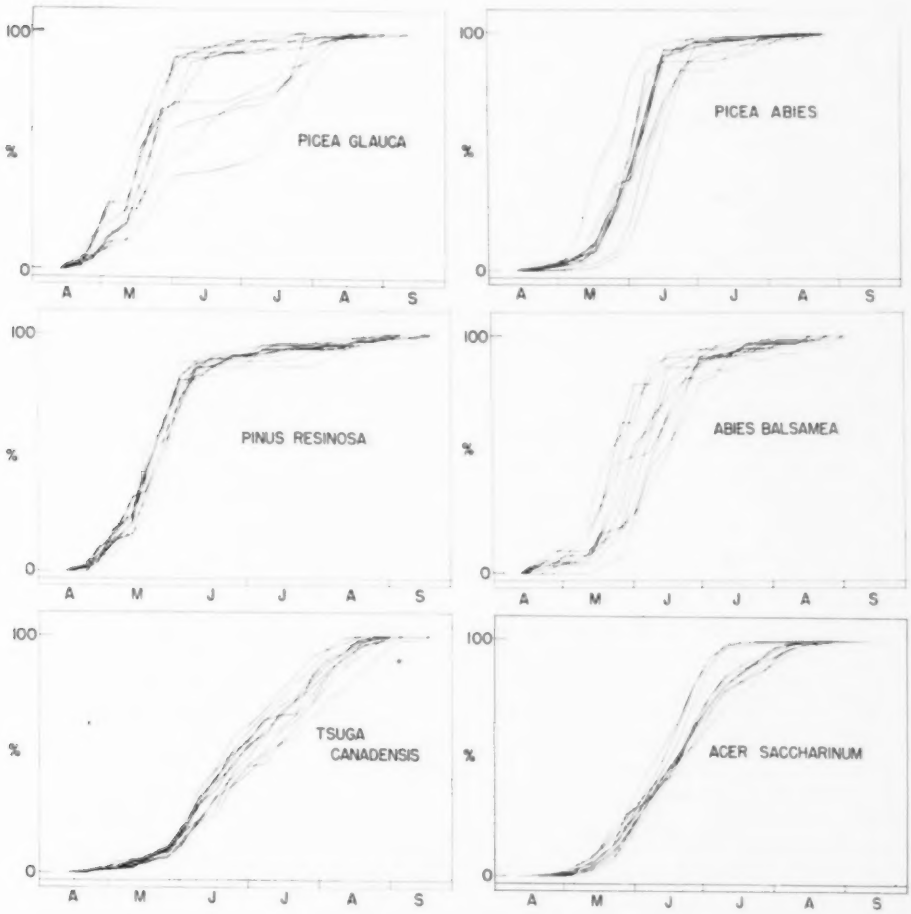
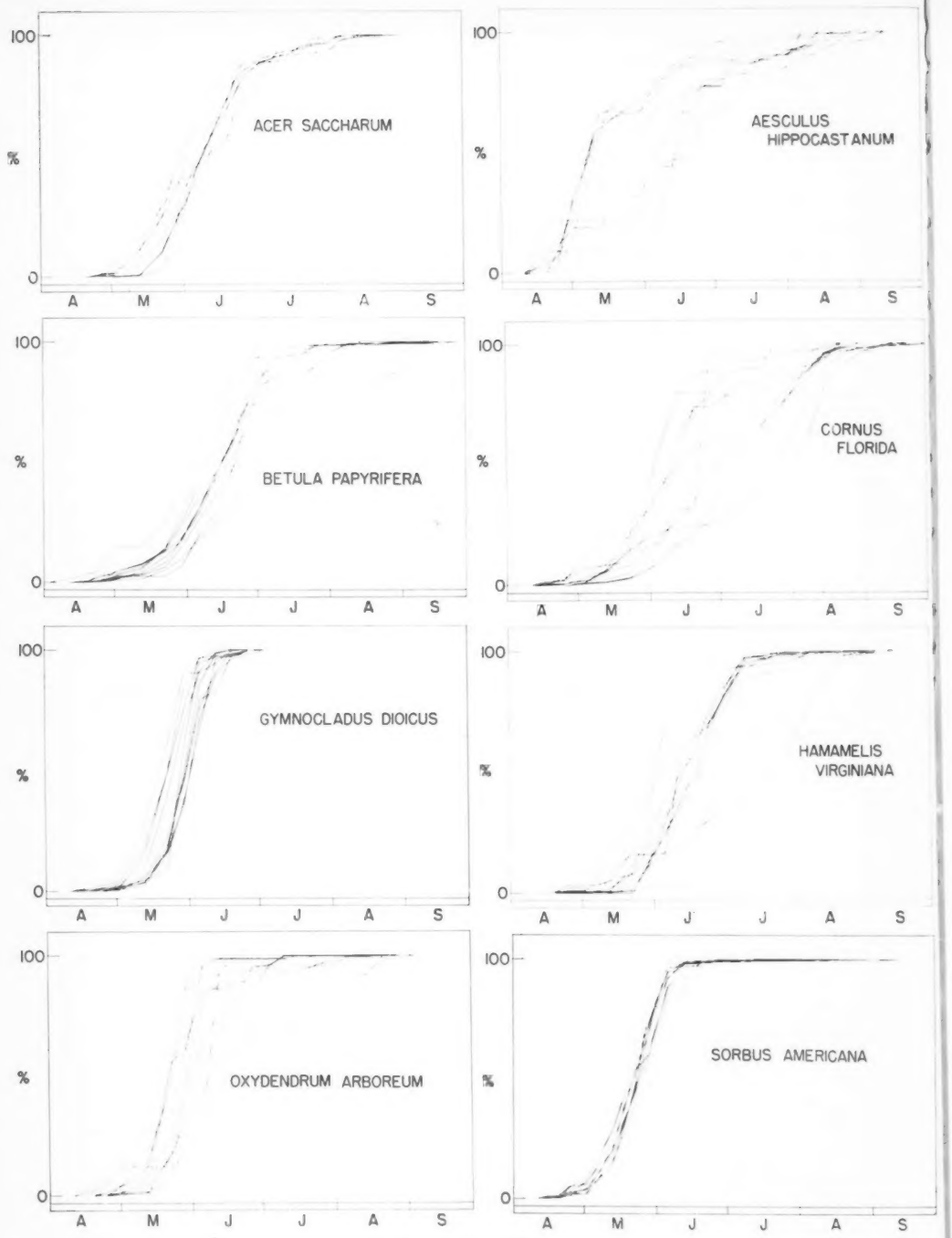


FIGURE 2. (*Above and on following page*) *The course of seasonal height growth of 10 seedlings of each of 5 species of gymnosperms and 9 species of angiosperms. The gymnosperms were grown in a forest nursery at Amherst, Mass. and the angiosperms at a nursery in Westfield, Mass. Height growth is plotted as percent of season's total completed at various dates.*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A M J J A S
ACER SACCHARUM
AESCULUS HIPPOCASTANUM
BETULA PAPYRIFERA
CORNUS FLORIDA
GYMNOCLADUS DIOICUS
HAMAMELIS VIRGINIANA
OXYDENDRUM ARBOREUM
SORBUS AMERICANA

FIGURE 2. (*Ctd.*)

Height growth. Variations in height growth of individual trees of different species suggest that growth studies often deal with essentially heterogeneous populations. In some species (red pine, mountain-ash) all seedlings measured showed a similar seasonal growth pattern. In contrast, in other species (balsam fir, dogwood) there was great variation in growth patterns of individual trees. Thus, a single curve for height growth of a species, based on averaged observations taken on a number of trees, gives no indication of the amount of within-species variation in growth. Such species growth curves are essentially artifacts since they give the impression that height growth is basically an uninterrupted process. The observations on which such curves are based usually are spaced so far apart that short-time changes in rates of growth are hidden and practically all published growth curves fail to show these short-time changes. Actually a distinct daily rhythm in shoot elongation occurs, with more height growth usually taking place during the night than during the day (Kramer and Kozlowski 1960). Mork (1941) found in eastern Norway that maximum apical growth of Norway spruce took place at night, whereas growth stopped or decreased during the day.

It is relatively easy to impose an artifact on a species growth curve by the reaction of a minority of the trees studied. For example, a seasonal growth curve for white spruce, based on averaged observations on ten trees, showed a distinct secondary growth burst after June (Kozlowski and Ward 1957a). Yet the majority of the seedlings measured showed no increased late-season growth.

The recurrent nature of shoot elongation has been demonstrated for sub-tropical and tropical trees which elongate, cease growing for a few weeks and then grow again (Reed and MacDougal 1937, Bond 1942, Greenwood and Posnette 1950). Such trees may flush several times during one growing season. Although somewhat less obvious, shoot growth of Temperate Zone trees also is intermittent and this can be demonstrated in various ways. Their height growth shows both seasonal and diurnal periodicity. Even when seasonal growth is plotted from observations widely spaced in time some trees show deviations from a smooth, sigmoid curve. As shown in the present study many trees show wide deviations from the average growth curve for a species.

Some trees grow while others are dormant and large variations in rate of growth commonly occur. Bimodal growth curves are not uncommon. These are sometimes associated with production of lammas shoots. Friesner (1942) plotted individual growth curves of four species of conifers growing in Indiana and found that he could classify seasonal height growth patterns into nine distinct curve types. His curves, which were plotted as weekly height growth over time, were rarely symmetrical. In some curves one side was drawn out longer than another. Others showed double peaks of varying intensity or of approximately equal intensity. Still others showed a flat plateau. In another study, Friesner (1943) measured seasonal shoot elongation of individual trees and found three distinct waves of growth in the same year with large deviations from a grand-period type of curve.

The hereditary control of the pattern of seasonal height growth has been well established(Kramer 1943). Height growth of many species does not respond readily to small fluctuations in environmental factors and height growth curves often are quite similar from year to year. Friesner (1942) showed that heavy rains in June failed to check declining growth of pines. However, height growth appears to be more sensitive to environmental control in some species than in others. Actually many factors influence the seasonal character of height growth. Among the most important of these are species (Kramer 1943, Kramer and Kozlowski 1960), age (Turner 1956, Wareing 1956), tree vigor (Merrill and Kilby 1952), morphological characteristics (Wenger 1955), seed source (Vaartaja

1954, Billings 1957), temperature (Hiley and Cunliffe 1922, 1923, Farnsworth 1955, Kramer 1957), current-year or prior-year soil moisture conditions (Pearson 1918, Burger 1926, Kramer 1943, Hustich 1948, Motley 1949, Kozlowski 1955, Kozlowski and Ward 1957a, 1957b, Kozlowski 1958, Kramer and Kozlowski 1960), light intensity (Gast 1930, Mitchell 1936, Kozlowski 1949), photoperiod (Wareing 1956, Downs and Borthwick 1956), soil physical properties (Coile and Schumacher 1953), soil chemical properties (Woodwell 1958, Kramer and Kozlowski 1960), and topography (Einspahr and McComb 1951).

There has been so much emphasis on similarity of height growth patterns and on sigmoid height growth curves that the impression has been conveyed that height growth is a continuous process. Much clearer responses can be demonstrated for diameter growth than for height growth, to current-season environmental fluctuations. To a considerable extent this is traceable to the relatively short growing season for shoot growth. By virtue of its short duration height growth often escapes severe environmental stresses such as late summer droughts (Kozlowski 1955, 1958). The present study has shown large variations in amounts and seasonal distribution of height growth of species and of individual trees. These variations occur under relatively little competition as well as with severe competition. Under the stratified conditions of a forest where competition is intense and microclimates vary greatly considerable variation may be expected in vigor and amount and distribution of growth of individual trees. There is only limited usefulness in comparing height growth curves of trees of varying age, on different sites and of varying vigor without some estimate or representation of variations of growth of individual trees from curves based on means of observations taken on several trees. The changes in rates of shoot growth appear to be more subtle than fluctuations in diameter growth but height growth, like other growth processes, is basically intermittent in character.

The variations in rates and patterns of growth of individual trees probably reflect individual differences in internal food, water, hormone, and mineral relations. Such correlations are conditioned by external factors acting on internal physicochemical processes and conditions. Since growth is physiologically ordered in the individual tree two trees of the same species often do not respond alike even to severe environmental changes.

Shoot elongation on different parts of trees. The amount of shoot elongation on different locations of a tree varies greatly. In red pine, white pine, white spruce and black spruce growth of the primary axis was greater than the average growth of secondary branches for the same year. However, growth of an individual secondary branch occasionally exceeded that of the primary axis, especially in the event of injury to the terminal shoot. Shoot elongation in secondary branches also decreased from the top of the tree downward. In white and red pine, growth of tertiary and quaternary axes also decreased from the upper to lower whorls of branches. In addition, when two sets of tertiaries were present on a branch, the set nearer the branch apex grew more than that farther down on the branch. A form of apical dominance occurs within branches as well as between branches. Thus growth of conifers tended to decrease progressively downward and inward in the four highest whorls of branches. The extremes in amounts of shoot elongation are pointed up in comparing growth of lowermost quaternary shoots and the terminal leader. On the average the terminal leaders of both red and white pines grew more than 10 times as much as the quaternary branches of their fourth whorls.

Variations in growth in different parts of the same tree are traceable both to differences in rate of growth and duration of growth of the various axes. Friesner (1943) reported that shoot elongation of

conifers began at approximately the same time on all branches over the entire tree contour. However, secondary axes showed successively shorter duration of growth and a slower daily growth rate from the topmost whorl downward.

Apical dominance in amounts of growth obviously controls crown form. In conifers the steepness in the gradient of growth from the primary axis to the secondary axes progressively lower down on the stem determines, to a large extent, the eventual form a conifer crown assumes. In contrast to the situation in conifers elongation of lateral shoots in many deciduous trees proceeds at approximately the same rate.

In conifers the large variation in shoot elongation on different parts of the same tree emphasizes a pronounced internal control of growth. The physiological mechanism of apical dominance is not fully understood but auxins and foods appear to be variously involved. Skoog and Thimann (1934) and Thimann (1937) attributed apical dominance to the inhibitory effect of auxin, which was produced in the terminal buds, on lateral buds lower down on the stem. These investigators were impressed by the observation that apical buds had higher auxin contents than other buds. When they removed apical buds lateral buds on the main stem grew immediately. However, the growth of such lateral buds could be prevented by applications of auxins to the cut ends of plants. Such experiments have been repeated many times on a wide variety of plants. However, the question of why growth of lateral buds should be inhibited by auxin alone while growth of the apical bud should not be similarly inhibited has been troublesome. According to Went (1936, 1939) growth of lateral buds is inhibited because of deficiency of both food and growth substances. Went suggested that food and growth substances were diverted to terminal buds which were regions of high auxin content. Camus (1949) showed that although apical buds inhibited lateral buds, auxin contents of apical and lateral buds were not significantly different. Furthermore, Champagnat (1955) demonstrated in *Syringa vulgaris* that the larger leaves, which contain little auxin, inhibit growth of lateral buds and that the terminal buds, which have a high auxin content, have a negligible inhibitory effect.

More recently attention has turned to nutritional implications in correlative growth inhibition. Gregory and Veale (1957) observed that the effect of auxin on lateral bud inhibition depends on the availability of carbohydrates and nitrogen for growth. They suggest that auxin plays an indirect role. The existence of internal competition for foods among meristematic tissues indicates that under conditions of nitrogen deficiency the most active meristems such as terminal buds monopolize the nitrogen supply and grow more than lateral buds. It appears that considerable research needs to be done before the basic physiological mechanisms underlying internal control of shoot growth are fully understood.

Summary

1. Ten randomly selected trees of each of five coniferous species and nine deciduous species of trees were measured for height growth at approximately weekly intervals in central Massachusetts during the growing season of 1954. Also elongation during 1960 of primary and secondary axes of two species of conifers and elongation of primary, secondary, tertiary and quaternary axes of four species of conifers was measured in central Wisconsin.
2. Based on averaged observations on several trees of each species some pronounced species height growth characteristics such as generally short, intermediate or long growing seasons were shown. Red pine and white spruce made rapid initial growth, but three out of ten white spruce trees showed a significant second burst of late season growth. In general Norway

spruce, balsam fir and eastern hemlock had longer growing seasons. Among the deciduous species mountain-ash and Kentucky coffeetree had short growing seasons; sugar maple, silver maple, witch hazel and sourwood had intermediate growing seasons; and paper birch, dogwood and horsechestnut had longer growing seasons.

3. Large within-species variations occurred either in the amount of shoot growth or in the distribution of seasonal height growth or both in some species. In Norway spruce the amount of growth of individual trees varied greatly, but in hemlock and balsam fir the variations in the amounts of growth among individual seedlings were much smaller. Relatively little variation occurred in the seasonal growth pattern of individual seedlings of mountain ash and red pine. In contrast, large variations in seasonal growth patterns among individual trees occurred in dogwood, paper birch, horsechestnut, witch hazel, sourwood, balsam fir, and white spruce.
4. Most published height growth curves are based on observations taken on a number of trees. Such height growth curves often are artifacts since they indicate that height growth is basically an uninterrupted process characterized by a sigmoid curve. Such curves obscure the short-time changes in rates of growth of individual trees and they obscure the large within-species variations in the amount and distribution of growth which often occur.
5. Large variations occurred in the amount of annual shoot growth on different parts of coniferous trees. The primary axis grew more than a secondary axis; a secondary axis grew more than a tertiary axis; and a tertiary axis grew more than a quaternary axis. Growth of a secondary axis was greatest at the terminal whorl and decreased progressively downward in lower whorls. Similarly shoot growth of tertiary and quaternary axes decreased from the top of the tree downward. When two sets of the same axis occurred on the same branch the set closer to the branch tip grew more than that located at a greater distance from the tip. Thus a downward and inward correlative inhibition of branch growth was shown.
6. Shoot elongation is fundamentally a variable and intermittent process. This can be demonstrated for southern and tropical species by recurrent growth flushes and for Temperate Zone species by short-time variations in rate of height growth, variations in seasonal distribution of growth of individual trees, and large variations in rate and duration of shoot growth on different parts of trees.

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Illustrated Genera of Wood Decay Fungi

By Charles L. Fergus. 135 pp., Illus. Burgess Publishing Company, Minneapolis 15, Minnesota. 1960. $4.

Review by Ross W. Davidson
Forest Service, U.S. Department of Agriculture

This is one of a series of books, in loose-leaf (spiral) binders, put out by Burgess on genera of fungi. They constitute numerous keys to families and genera. This one by Fergus is confined to Hymenomycetes which occur on or cause disease or decay of trees and wood. The title implies that the genera included are wood decay fungi but numerous genera are included, such as *Exabasidium*, *Septobasidium*, and *Aleurodiscus*, which are present on living trees but cause little or no damage to the wood. From the standpoint of the student this broad coverage may be of considerable advantage since the author states that no information is given on effect of the fungi on the substratum.

The first key is to 9 families of Hymenomycetes. To 8 of these families are assigned the common names, "gill fungi," "pore fungi," "toothed fungi," "coral fungi," "smooth fungi," and 3 are of the "jelly fungi." In Agaricaceae (gill fungi) where many genera grow only on soil just the genera with some species on wood are included. The second key is constructed from generic characteristics irrespective of family groupings. It is a large "Supplemental key to . . . genera" and occupies 10 pages. As each genus is keyed out the name is followed by a number in parenthesis—the genus number. Such numbers also correspond to numbers of figures or illustrations which are consecutively arranged. Keys to genera of individual families are also inserted throughout the book and these are often followed by short keys to the species of important genera. However, no definite procedure is followed, for as with the Polyporaceae there is a key to genera and a 9 page "key to species," except for species of *Poria* which constitutes a large group difficult to diagnose on a species basis.

The most valuable feature of the book consists of the very excellent illustrations, mostly photographs. There are 81 numbered illustrations with each genus being typified by a particular species. For some there are 2 to 3 photographs—one of the upper surface and the other of lower surface of basidiocarps showing hymenial features such as pores, gills, teeth, etc. Thus the student is given much information on some of the important species encountered.

At the end of the keys there is a list of references which includes monographs asd papers giving more detailed information on the fungus classification. As is stated in the book, no information is given on amount or type of decay damage by individual species or genera, but the reader is referred to textbooks by Boyce and Baxter. A glossary of terms, and an index to genera, giving both generic and page numbers renders the book more useful. The arrangement and presentation is mainly for students in forest pathology but may be useful for foresters having a special interest in the fungi he encounters.

Liquid Dispersion Method for Mounting Wood Fibers on Slides

Note by R. M. Echols[1]
Southern Forest Experiment Station

In mounting wood fibers on slides for study under magnification, a number of problems are encountered that may affect mensurational accuracy. The usual procedure of selecting fibers for mounting after maceration and staining consists of either picking up a sample in liquid with a pipette, or removing a cluster of fibers from the liquid with forceps. Either method introduces bias in selection as well as breakage of fibers from mechanical spreading on the slide with a probe or needle. The ideal sample is well mixed, is evenly dispersed, and contains a minimum of broken fibers or fragments caused by severe treatment. A dispersion method meeting these criteria has been used as a standard technique at the Southern Institute of Forest Genetics of the Southern Forest Experiment Station for large numbers of wood samples.

Wood samples are split longitudinally into "matchstick" slivers about 1 mm square and placed in vials which are then filled with Jeffrey's macerating fluid (equal parts of 10 per cent nitric acid and 10 per cent chromic acid). The fluid is allowed to act at room temperature until the fibers separate easily, usually after 24 to 36 hours for pine summerwood.

When the maceration has progressed sufficiently, the fluid is poured off and replaced with water. A small piece of fine-mesh stainless steel wire gauze is shaped into a strainer which is placed over the mouth of a vial and held in position while the liquid is poured off. The strainer prevents escape of the macerated material and greatly speeds washing operations.

Water in the vials is changed several times over a 48- to 64-hour period, until no trace of the yellow acid can be seen, and the fibers are a gray-white. The last change of water is then poured off and replaced with a saturated aqueous solution of basic fuchsin, which is allowed to stand overnight. Finally, the stained fibers in the vials are washed with one change of water and are ready to be mounted on slides.

[1]The author is now principal Research Forester for Cooperative State Experiment Station Service, U. S. Dept. Agric., Washington 25, D. C.

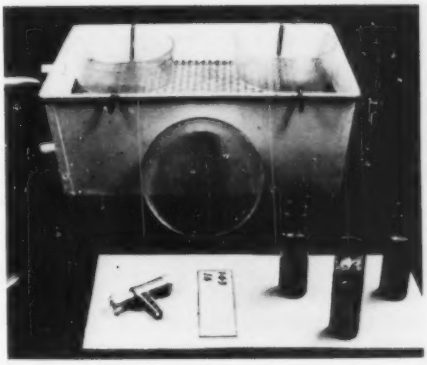

FIGURE 1. *Modified metal pan with wire-mesh tray and plastic containers. In foreground are hose clamp, numbered slide, and vials containing wood fibers.*

The principle of water dispersion involves the thorough distribution of a relatively large amount of fibrous material in a much larger volume of water. The dispersed fibers are then allowed to settle at random, thereby covering one or more slides placed at the bottom of the container. The water is drained off slowly so as not to disturb the positions of the fibers on the slides. A metal pan is modified by installing an overflow vent near the upper edge and a drain at the bottom, equipped with a cut-off valve and a metered orifice to control the rate of drainage (Fig. 1). A segment of rubber hose, a hose clamp, and a pipette is satisfactory for this drain. A wire-mesh tray is suspended in the pan about one inch below the overflow vent. Round plastic containers for the slides and fibers are adapted by drilling $\frac{1}{16}$-inch holes spaced about $\frac{1}{2}$ inch apart around the periphery of the bottoms to provide uniform drainage.

The pan is filled with water to the level of the overflow vent. The perforated containers are placed on the tray and allowed to fill with water. Clean glass slides are placed in the containers. A generous sample of stained fibers is deposited in each container, agitated gently with a stirring rod until uniformly dispersed through the liquid, then allowed to settle to

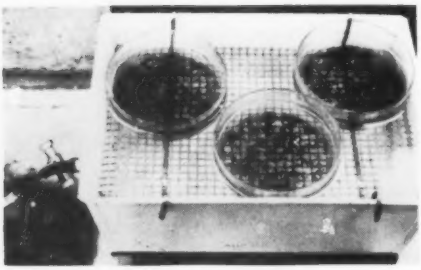

FIGURE 2. *Wood fibers in containers have been allowed to settle evenly onto slides.*

the bottom in an even layer (Fig. 2). The water is drained off very slowly by removing the hose clamp. After the water has receded from the containers, the slides are lifted out and blotted once, and cover slips are mounted. Sodium silicate solution (40°–42° Bé) is used as a mounting cement for semipermanent slides, since it is water-miscible and does not allow bleeding of the stain from the fibers [2] Sodium silicate hardens quickly around the edges of the cover slips so that the slides can be handled within a few minutes after preparation. Glycerin is a satisfactory mounting medium for temporary slides; they can then be washed and reused.

The liquid dispersion method permits adjustment of the density of numbers of fibers by adding to or removing from the containers. The pattern of dispersion can be changed repeatedly by restirring the liquid until desired uniformity is achieved. The technique permits measurement of the natural dimensions of wood fibers, i.e., they are not distorted by dehydration at any stage. In the event that dehydration is desired, the fibers are prepared with a standard dehydration technique, and an anhydrous liquid such as xylene is substituted for the water in the pan. Care should be taken to use containers that are not soluble in xylene, and to cover the pan to avoid noxious fumes and excessive evaporation.

[2] Echols, R. M. Variation in tracheid length and wood density in geographic races of Scotch pine. Yale Univ. School of Forestry, Bull. 64. 63 pp. 1958.

The Natural Regeneration of Eucalyptus regnans

By T. M. Cunningham. Bulletin 1, School of Forestry, University of Melbourne, Australia. 25 shillings.

Review by F. S. Baker, Professor of Forestry, Emeritus University of California.

The appearance of an outstanding bulletin (140 pages of text, 25 excellent illustrations, plus 11 short appendices consisting mainly of statistical tabulations) marks the initiation of forest research publications from the School of Forestry at Melbourne, Australia.

It is interesting indeed to read this publication, for it takes us into a very unfamiliar forest and discusses ecological problems that may have their counterparts in our own country or which may turn out to be new and different.

The species of eucalyptus considered here, commonly called mountain ash in Australia, is certainly very far from the familiar "mountain ash" of the United States, for as Cunningham states: " . . . dominant heights between 180 and 250 feet are usual in stands over 100 years in age." Two stand tables representing areas upon which studies were made are also presented. The younger stand, representing the approximate age class of the mature managed stand of the future, was 65 years old. The stand ran 105 trees per acre, the mean height of dominants was 134 feet, and d.b.h. ranged from 8 to 30 inches. The virgin forests now being logged are, of course, older and the one studied most fully evidently originated from fire 165 years previously. Here there were 31 trees per acre, the mean dominant height was between 200 and 260 feet, and diameters ran from 42 to 96 inches at breast height. Clean stems to the first living branches averaged about 150 feet.

These striking stands of nearly pure moun-

tain ash have apparently developed as even-aged forest following fires largely in the mountains at elevation of 1500 to 3500 feet, in a climatic zone where precipitation amounts to 50 to 80 inches per year and is fairly well distributed seasonally, although there does seem to be a rather regular summer dry period of short duration. Light snows are common in the winter. The mountain ash is very intolerant of shade and as the stands develop and approach maturity there develops a well defined understory of tolerant hardwoods of small value, associated with shrubs and herbaceous growth of the same character.

These magnificent stands develop rapidly and will yield heavy timber crops in about 100 years, but as the title of the publication clearly indicates, regeneration is by no means simple in managed stands. The original, natural method by fire running through existing stands is, of course, quite impossible to the forester. Some reasonably cheap and truly effective method needs to be developed. This publication describes the studies carried on for this purpose.

In the first place the seed crops are surprisingly small: only about 100,000 seeds per acre in the virgin forests. These seeds are tiny (about 1,000,000 to the pound) and are borne in the type of capsule found in all eucalypts. These capsules dry out and open rather slowly and irregularly so that seed dissemination is uneven. And, of course, the seed falls directly beneath the crown of the seed-bearing tree. In the second place, this study revealed that approximately 80 percent of this small crop is harvested by insects—mainly ants. The unharvested seed germinates well upon mineral soil in the spring but only 5 to 20 percent of the first-year seedlings pull through the initial year, the greatest death loss coming in the first winter apparently from soil fungi. At the same time there is also summer loss from high soil temperatures and top-soil drouth, just as we have in our country. As a result of all these things, Cunningham concludes that no more than ½ to 1 percent of the annual seed crop will develop into established seedlings if a mineral seed bed is developed. If there is no mineral soil exposed, the regeneration will be nothing at all.

From this study it becomes evident that to insure the production of mountain ash there needs, first of all, to be the assurance of more seed production. Cunningham discusses ways of increasing the numbers of seed trees, partial cutting of the stands, strip and patch systems of felling, possible increase in seed-tree productivity, and artificial reseeding. Then obviously comes control of seed-robbing insects, the improvement of the seedbed (mineral soil) and the development of some overhead shelter to guard against summer season losses.

Not only is this a well developed silvicultural story of a type of forest very new to us but the publication is very interesting as we look at the research methods employed in the field upon an area not very accessible to the workers. Many of the means of attack on the problems should be of interest to Americans working under similar circumstances; also, it is interesting to note that Cunningham borrowed freely from our own methods. Indeed, he goes so far as to state that he sees much similarity between mountain ash and Douglas-fir in problems of regeneration for the assurance of well-stocked, even-aged stands promptly after logging.

The publication carries a list of 63 references, of which 32 are Australian or Tasmanian, and are largely concerned with the silvics of *Eucalyptus regnans* and other eucalpts. Twenty-seven references are from the United States and Canada—mostly from the Pacific coast. There remain four rather lonely references from European sources. The whole publication brings out the fact that American and Australian forest research are very closely allied and both groups can learn much from each other.

Minnesota Lands

By Samuel Trask Dana, John H. Allison, and Russell N. Cunningham. 463 pp. The American Forestry Association. Washington, D. C. 1960. $5.

Review by Z. A. Zasada
Forest Service, U. S. Department of Agriculture

Covering ownership, use, and management of forests and related lands this book is a report on one of the American Forestry Association's state studies of forest land ownership. It is a well documented report of one of the most complex patterns of land ownership in the United States. Although the authors review the forest land ownership for the State of Minnesota as a whole, the results are focused on conditions in the northern forest area, which includes the 16 northeastern counties.

The authors are ideally qualified to make the study. J. H. Allison, professor emeritus, School of Forestry, University of Minnesota, and R. H. Cunningham, formerly chief, Division of Forest Economics, Lake States Forest Experiment Station, have been associated with surveys and studies of Minnesota's forest land problems for many years. S. T. Dana, dean emeritus, School of Natural Resources, University of Michigan, with wide experience in the field of natural resources, gave the "team" unbiased leadership for the study. An advisory committee of local forestry and conservation leaders, provided a "grass roots" background for the study.

The story is presented in four parts: I. Natural Resources and People; II. Evolution of Land Ownership; III. Present Pattern of Land Ownership; IV. Problems and Prospects. A very detailed appendix includes land statistics, reports on forest land conditions and management in two counties, and a compilation of tax and land ownership legislation add to its value as a reference book. The first three sections provide the background material for the discussion of results in part IV, "Problems and Prospects."

To readers not acquainted with Minnesota it will be helpful to point out that the northern forest area includes most of Minnesota's 10,000 lakes, iron ranges, and wildlife resource. During the last decade this area has seen a sharp decline in agriculture and foreign ores are becoming increasingly competitive with local ores. The forests with the associated resort and recreation business offer the brightest prospects for economic expansion.

The authors trace the evolution of land ownership from the time of the coming of the white man, through Indian treaties, homesteading, land grants, land forfeitures, and changing federal, state and county land policies. The story is interesting and well told.

The significant point in the pattern of present ownership is that the majority of the forest lands are in public ownership almost equally divided between the county, state, and federal governments. A substantial part of this public ownership was privately held at one time. These circumstances make Minnesota forest land ownership different from most states.

The key section of the book to most readers is part IV, "Problems and Prospects." Here the authors present their conclusions. Anyone familiar with the Minnesota forestry situation during the past few years will agree that the authors have done an excellent job in presenting the specific problems of each class of ownership. The recounting of the wide range of problems as status of land holding, contributions to local communities, timber sale policies, income from land, intensity of land management is done in such a way that help explain the situation as a whole. Many readers will not agree with all proposed solutions, but the authors do present the facts which will help to speed solutions.

This book is an important forestry contribution to the State of Minnesota. It will serve as a reference volume for years to come. The book is timely, being published at a time when forest land ownership is receiving increasing public attention in Minnesota. The book is recommended to all conservationists interested in forest land management.

Dry-Matter Content of Loblolly Pine Needles Appears Unrelated to Geographic Seed Source

BY
B. F. McLEMORE
A. B. CROW
P. C. WAKELEY

VARIATIONS IN dry-matter content of needles, found highly useful by Langlet (1936-37, 1959) as an indicator of racial variation in Scotch pine (*Pinus sylvestris* L.), appears to offer little or no promise of similar utility with loblolly pine (*P. taeda* L.)

The existence and the economic importance of racial variations in southern pines, particularly loblolly pine, have been demonstrated beyond question (Bercaw 1955; Sherry 1947; Wakeley 1944, 1954, 1959; Zobel and Goddard 1955). A Southwide study of geographic sources of seed of longleaf (*P. palustris* Mill.), slash (*P. elliottii* Engelm.), loblolly, and shortleaf (*P. echinata* Mill.) pines was begun in 1951 to define seed-collection zones for these species (Wakeley 1959). Of necessity, however, the geographic sources represented are so widely separated that boundaries of collecting zones will be only roughly determinable from the data.

To test the possibilities of supplementing and refining results by means of Langlet's technique, dry-matter contents of needles of the previous year were determined in 1957 for loblolly pines of various geographic origins. Table 1 lists the seed sources and the locations of the plantations. The sources represent very nearly the extremes of latitude, longitude, and climate within the natural range of loblolly pine. Unless dry-matter content of needles varied significantly and consistently among the sources representing these extremes, it could not be expected to indicate racial variations occurring within more limited portions of the range, and hence could not be used to refine results based upon outplantings.

Trees in Pearl River County, Mississippi, were sampled shortly after the start of their fifth growing season in the plantation and sixth from seed. Those in Rapides Parish, Louisiana, were sampled during their 21st growing season in plantation. Circumstances precluded sampling in the dormant season, as preferred by Langlet (1936-37), but Scotch pine gave indicative differences at other seasons also; and Meyer (1928, 1932), working with pitch pine (*P. rigida* Mill.) in Ohio, where the environment is more like that of loblolly pine than of Scotch pine, found the moisture content of mature needles about the same in winter as in summer.

Preliminary tests were run to develop techniques that would minimize variations in dry-matter content arising from collection, transportation, preparation, and drying of samples. Then on April 27, comparable needle samples were collected from 4 trees in each of 4 replications of each source in each series in the Pearl River County plantations. On June 18 samples were collected

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Portion of a thesis submitted by the senior author in partial fulfillment of the requirements for the M.F. degree, Louisiana State University. McLemore and Wakeley are members of the Southern Forest Experiment Station, Forest Service, U. S. Department of Agriculture. Crow is Associate Professor of Forestry, Louisiana State University, Baton Rouge, La. Manuscript received Jan. 27, 1961.

similarly from 4 trees in each of 3 replications of each source in the Rapides Parish plantation.

Samples were dried at 65°C for 48 hours in an electric oven. Following Langlet, dry-matter content was computed as a percentage of fresh weight, equaling

$$\frac{\text{oven-dry weight}}{\text{fresh weight}} \times 100.$$

Mean percentages were calculated for sources and for replications within sources. The latter were subjected to analyses of variance, the former (shown in Table 1) to regression analyses.

The dry-matter contents of sources did not vary significantly in series 1 in Pearl River County, or in the Rapides Parish plantation. Variation among sources in series 2 in Pearl River County was significant at the 5-percent level but was not correlated with latitude of source. In fact, no relationship could be found between differences in dry-matter content and climatic conditions at the various points of seed collection. Specific variables investigated were mean annual precipitation, mean January and July temperatures, length of growing season, and (in an attempt to approximate moisture stress), mean annual precipitation divided by July temperature. Nothing directly involving climate suggested itself as an independent variable over which dry-matter content regressed. Series 2 in Pearl River County suggested a possible association of dry-matter content with physiographic province of seed source, but this was refuted rather than confirmed

TABLE 1. Proportionate dry-matter content of needles from various sources.

Pearl River County, Mississippi		Rapides Parish, Louisiana	
Source by county	Dry matter	Source by county	Dry matter
	Percent		*Percent*
Series 1: Range in latitude from 30°30′ to 38°10′ N. Range in longitude from 75°45′to94°40′W.		Range in latitude from 30°15′ to 38°25′ N. Range in longtitude from 75°40′ to 95°30′ W.	
Angelina, Tex.	44.50	Trinity, Tex.	48.22
Onslow, N. C.[1]	43.53	Ashley, Ark.	47.65
Clark, Ark.[1]	43.13	St. Tammany, La.	47.61
Somerset, Md.	43.06	Natchitoches, La.	47.42
Pamlico, N. C.	42.99	Edgefield, S.C.	47.37
Wilcox & Crisp, Ga.	42.99	Winston, Ala.	46.95
Clay, Ala.	42.60	Leon, Fla.	46.88
Livingston, La.[1]	42.52	Wicomico, Md.	46.54
		Montgomery, Tex.	46.51
Series 2: Range in latitude from 30°30′ to 35°10′ N. Range in longtitude from 77°30′ to 93°15′ W.		Onslow, N.C.	46.37
		Jefferson, Miss.	46.31
		Charles City, Va.	45.63
Onslow, N.C.[1]	43.76		
Livingston, La.[1]	43.30		
Clark, Ark.[1]	42.78		
Prentiss, Miss.	42.76		
Jefferson, Ala.	42.60		
Hardeman, Tenn.	42.58		
Newberry, S.C.	42.36		
Clarke, Ga.	41.54		
Spalding, Ga.	41.31		

[1]Common to series 1 and 2 in Pearl River County.

by the Rapides Parish results.

Dormant-season retrials may be warranted with loblolly or other southern pines. It is surmised, however, that the contrast between Langlet's results and those reported here is attributable primarily to the greater importance of low temperatures in the evolution of Scotch pine, which occurs at higher latitudes than loblolly pine.

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DISTRICT OF COLUMBIA

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YOUNG W. RAINER, *Business Manager*

Sworn to and subscribed before me this 12th day of September, 1961 (seal). Spencer T. Money, Notary Public, Washington, D. C. (My commission expires May 15, 1969.)

Influence of Cycloheximide on Growth of Mycorrhizal Fungi and on Mycorrhizae of Pine

BY
EDWARD HACSKAYLO

CONTROL of white pine blister rust, caused by the fungus *Cronartium ribicola* Fischer, can be achieved through the use of antibiotic, cycloheximide. The methods used for application of the antibiotic to affected western white pine trees were described by Moss *et al.* (1960),[1] who warned that, although control of the disease has been phenomenal on this species, the possibilities of deleterious side effects should be fully explored.

I have attempted to determine whether cycloheximide has a deleterious effect on the mycorrhizae of pine when the antibiotic is applied to the stems. The investigation was divided into two parts: (1) the effects of cycloheximide on the growth of selected fungi that are known to be associated with the mycorrhizae of pine and (2) observations of the mycorrhizae of eastern white pine (*Pinus strobus* L.) plants growing in the greenhouse after applications of cycloheximide[2] to the stems.

The Effects of Cycloheximide on Fungi in Vitro

Ten species of fungi were grown for 4 weeks at 21°C in Petri dishes on agar containing the following: KH_2PO_4, $MgSO_4 \cdot 7H_2O$, and NH_4Cl, 0.5 gm each; malt extract and glucose, 5.0 gm each; 1% solution of ferric citrate, 0.5 ml; agar, 15.0 gm; distilled H_2O to make 1000 ml. The colonies were cut into pieces approximately 5 mm square with a sterile scalpel. The pieces were then transferred to dishes of fresh medium. After 48 hours the squares on which new growth had started were ready to use as inoculum. Meanwhile, additional nutrient agar was prepared and divided into six portions. Cycloheximide in an aqueous stock solution that had been sterilized by passage through a bacteriological filter was added to five portions of agar that had been melted and cooled to 40°C. The following concentrations of cycloheximide were thus prepared: 1000 ppm, 100 ppm, 10 ppm, 1 ppm, and 0.1 ppm. No cycloheximide was added to a sixth portion, which served as a control.

Plates were poured with approximately 20 ml of the prepared agars per plate. After the agars solidified one square of inoculum was transferred to each plate. Three replicates of each fungus species were implanted on agar containing each concentration of cycloheximide and on the control agar. The cultures were maintained at 21°C and the diameters of the colonies were measured after 4 weeks. The average colony diameters of the fungi grown at each concentration of cycloheximide are given in Table 1.

The concentration of cycloheximide having a significant effect upon growth

[1] Moss, V. D., H. J. Viche, and W. Klomparens. Antibiotic treatment of western white pine infected with blister rust. J. For. 58: 691-695. 1960. (*Editor's Note*: See also pp. 380-396 this issue of FOREST SCIENCE.)

[2] The Acti-dione crystalline antibiotic used in the experiments described in this paper was supplied by the Upjohn Company.

The author is a plant physiologist, Forest Physiology Laboratory, Forest Service, U. S. Dept. Agric., Beltsville, Md. Manuscript received Dec. 30, 1960.

TABLE 1. Average colony diameters of mycorrhizal fungi grown on agar without and with cycloheximide in the medium. The initial diameter of the inoculum was 5 mm.

Species	Colony diameter for indicated concentration (ppm) of cycloheximide					
	0	0.1	1	10	100	1000
	mm					
Cenococcum graniforme (Sow.) Fred. and Winge	29 a[1]	27 b	27 b	26 b	11 c	5 d
Boletus felleus Bull.	68 a	69 a	69 a	45 b	5 c	5 c
Amanita rubescens Fr. 1	39 a	34 b	31 c	23 d	5 e	5 e
A. caesaria Fr.	54 b	57 a	34 c	17 d	5 e	5 e
A. verna Fr.	56 a	56 a	37 b	15 c	5 c	5 c
A. flavorubescens Atkins.	17 a	18 a	13 b	10 c	5 d	5 d
A. rubescens Fr. 2	51 b	60 a	45 c	5 d	5 d	5 d
A. muscaria Fr.	34 a	32 a	27 b	5 c	5 c	5 c
Boletus rubellus Krombholz	37 a	40 a	23 b	5 c	5 c	5 c
Russula emetica Fr.	38 a	34 b	21 c	5 d	5 d	5 d

[1] For comparisons within species, numbers followed by different letters are significantly different at the 1 percent level.

varied among species of fungi. The two isolates of *Amanita rubescens* grew differently under the control conditions. In addition isolate 2 of *A. rubescens* was stimulated by 0.1 ppm cycloheximide as was *A. caesaria*. All the fungi were completely inhibited at either 10 or 100 ppm cycloheximide (Fig. 1) with the exception of *Cenococcum graniforme*. This fungus is more tolerant of the antibiotic since complete inhibition occurred only at the concentration of 1000 ppm. The species of all genera were sensitive to the antibiotic, but sensitivity varied considerably among species within any genus. Most species used in this experiment showed initial depression of growth at 1 ppm.

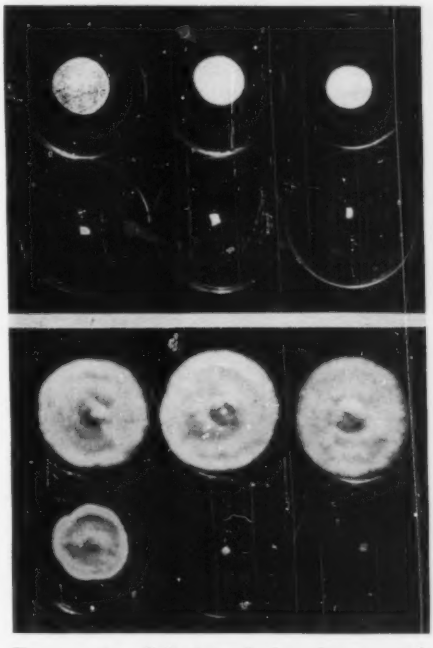

FIGURE 1. *Colonies of* Amanita muscaria (*above*) and Boletus felleus (*below*) *grown for 4 weeks in agar containing cycloheximide as follows:* (*Left to right in each photograph*) *top row, 0 ppm, 0.1 ppm, 1 ppm; bottom row, 10 ppm, 100 ppm, and 1000 ppm.*

Stem Application of Cycloheximide to Eastern White Pine

Two-year-old eastern white pine trees were obtained from a local nursery in September 1959 and were planted in 7-inch pots containing sterilized soil which was then inoculated with leaf mold from a pine woods. Inoculation insured the presence of mycorrhizal fungi. The trees were grown in the greenhouse on 18-hour photoperiods.

By March 1960 the trees were well established and roots had grown to the sides

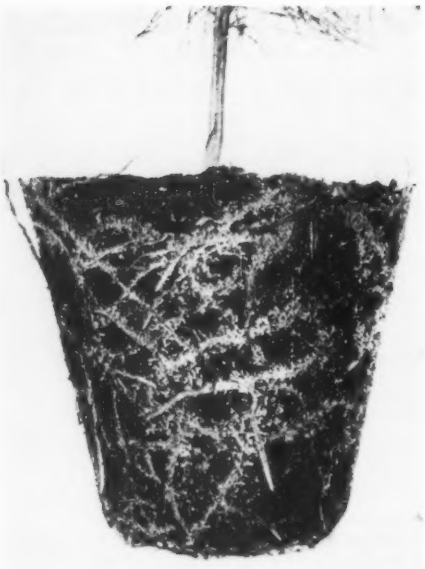

FIGURE 2. *Mycorrhizae on the roots of an eastern white pine seedling. Ninty days previously the seedling had received a stem application of 500 ppm cycloheximide in No. 1 fuel oil.*

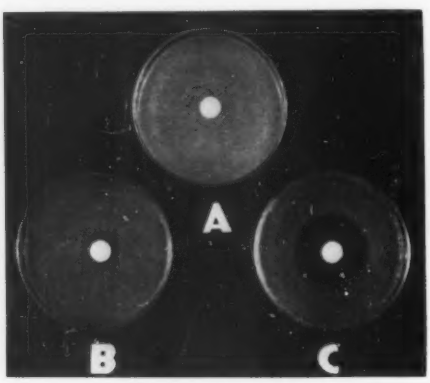

FIGURE 3. *Response of* Saccharomyces pastorianus *seeded in nutrient agar to extracts of bark of white pine: A. Bark treated 90 days previously with No. 1 fuel oil. B. Bark treated 90 days previously with No. 1 fuel oil containing 500 ppm cycloheximide. C. Bark treated a few minutes previously with No. 1 fuel oil containing 500 ppm cycloheximide.*

of the pots. Ectotrophic mycorrhizae were well developed, and the roots were actively growing. The basal portions of the stems between the lowest needles and the soil were treated with solutions of cycloheximide as follows: The crystalline antibiotic was dissolved in a small amount of acetone and then diluted to 500, 250, and 125 ppm in No. 1 fuel oil. Fifty microliters of each solution and of fuel oil alone were applied to 5 trees.

The amount of cycloheximide deposited on the stems was 25.0, 12.5 or 6.25 micrograms per plant. The solutions and fuel oil were not permitted to contact the needles or the soil. Five trees were left untreated. Ninty days after treatment the plants were examined and harvested.

No apparent differences were noted on either the above or below ground portions of the plants. Mycorrhizae were well developed in all treatments (Fig. 2). Extracts of portions of the plants were made with water and methylene chloride to determine whether the antibiotic could be detected. The general procedure for extraction was described by Lemin *et al.* (1960).[3] The extracts were chromatographed, and the papers placed on agar that had been seeded with *Saccharomyces pastorianus*.[4]

At R_f 0.5 inhibition of the assay organism by cycloheximide was detected in the samples of treated bark from trees that had received applications of 25 micrograms. No inhibition was evident from comparable untreated bark extracts. Figure 3 illustrates inhibition of *S. pastorianus* by use of filter paper assay disks. No attempt was made to determine amounts of the antibiotic recovered. I was unable to detect

[3] Lemin, A. J., W. Klomparens, and V. D. Moss. Translocation and persistence of Cycloheximide (Acti-dione) in white pines. For. Sci. 6: 306-314. 1960.

[4] The nutrient formula and test organism were provided by the Research Division of the Upjohn Company.

the antibiotic in extracts of needles, untreated bark, wood, or roots from treated trees. Since there was no apparent damage to mycorrhizae at the highest concentration, no attempt was made to extract cycloheximide from trees that were treated with smaller amounts.

Discussion and Conclusions

It is significant that the several species of mycorrhizal fungi were inhibited in vitro by certain concentrations of cycloheximide. These results are not necessarily comparable to applications of the antibiotic to soil, but they do alert us to possible implications when such chemicals are applied to the soil. These data also suggest that the concentration of the antibiotic in the root tissues would have to be high to have a direct effect on the associated fungi.

It is not surprising that the mycorrhizae incurred no damage after applications of cycloheximide to the pine trees. Upward translocation of the antibiotic as reported by Lemin *et al.* (1960), would tend to prevent accumulation in the roots in sufficient quantities to be toxic to the mycorrhizal fungi. Any effect on the fungi would probably be indirect, due to interference in the metabolism of the host plant.

Timber Utilization in Malaya

Malayan Forest Records No. 13. Revised and expanded by specialist officers of the Forest Department in the Federation of Malaya and Singapore. Edited by C. O. Flemmich, formerly Forest Officer at Singapore. 1959. Printed by A. G. Banfield, Government Printer, Singapore. $6 (Malayan) or 14s (Sterling).

Review by B. Francis Kukachka
Forest Products Laboratory
Madison, Wisconsin

This highly useful book of 141 pages is not intended to replace standard text books on Malayan timbers but to bring up-to-date information and data accumulated since the first edition of June 1940. Over the 20-year period, considerable advances have been made in both forestry and timber utilization in the tropics and the latest work should be a handy volume for reference for anyone whose interest lies in this area. Although the book deals with Malayan species, the recommended practices outlined can be applied to any part of the tropics of the world.

The uninitiated will find the text easy to read since technical nomenclature is kept to a minimum and when used is described in simple terms generally accompanied by excellent illustrations. Photographs have been liberally used and their reproduction is of the highest level.

The text is divided into 10 chapters as follows: I Forestry in Malaya; II Anatomical Structure of Wood; III Identification, Classification, Spot Characters and Uses of Malayan Timbers; IV Seasoning of Timber; V Defects in Timber; VI Wood Preservation; VII Strength of Timber; VIII Destructive Agencies of Timber and Their Defeat; IX Grading and Purchase of Sawn Timber; X Plywood and Other Composite Wood Products. Chapter VIII contains a section on the correct design and utilization of timber in buildings—a very important consideration in tropical construction. It seems that the Malayan home owner is not only faced with the task of combating the usual pests bent on destroying his home, but periodically removing fig trees from his roof before appreciable damage can be done by this rather unique pest.

Some 11 specialists contributed to the production of this manual and coupled with the wide experience and able editorship of C. O. Flemmich, they have introduced an outstanding and very noteworthy manual.

Antibiotics for Control of Blister Rust On Western White Pine

BY
VIRGIL D. MOSS

FOR MANY YEARS, pathologists have been searching for a systemic fungicide to save white pines infected with blister rust, *Cronartium ribicola* Fischer. Heretofore, the disease was controlled only by destroying all alternate host plants (*Ribes* spp.) within white pine stands and in a surrounding protective zone about 1,000 feet wide.

The incentive to develop a chemotherapeutant and/or prophylactic for western white pine, *Pinus monticola* Dougl., arose from the needs to (1) save all infected high-value white pine stands to help meet future demands for softwood timber, (2) greatly expand the present acreage of western white pine benefiting from blister rust control, through cheaper and more effective direct control methods, (3) immunize against blister rust infection, nursery-grown seedlings for early reforestation, and (4) immunize against new blister rust infection the established stands that are being treated to save the diseased white pines in the Rocky Mountain region.

In an analysis of western white pine management, Matthews and Hutchinson (1948) showed that blister rust must be suppressed on 1,901,000 acres to maintain an annual cut for the next 80 years somewhere near the level of 200 to 300 million board feet, and an eventual annual cut after 80 years of 500 million board feet. The present rate of progress in ribes eradication will provide protection from blister rust on only 900,000 acres. This acre-volume deficit has presented a real challenge to the successful management of western white pine.

With the discovery of two antibiotics to control blister rust, foresters now have the assurance that western white pine can be successfully grown and managed in the northern Rocky Mountains. The antifungal antibiotics, cycloheximide and phytoactin, were discovered among 66 compounds selected, out of several hundred investigated, for testing on western white pine infected with blister rust. The screening tests and the results of the studies to develop formulations and methods of applying the antibiotics to western white pine are reported in this paper.

Literature Review

A historical review of the various attempts to develop a chemical treatment for white pine blister rust would serve little purpose here, because, as far as can be determined, all such experiments were unsuccessful up to 1949.

The author is Research Forester, Division of State and Private Forestry, Northern Region, Forest Service, U.S. Department of Agriculture. Manuscript received Mar. 8, 1961.

For assistance and materials provided for this study, acknowledgement is due to the following firms: Upjohn Company, Pabst Brewing Company, Chas. Pfizer Company, Olin Mathieson Chemical Corporation, Merck Company, Rohm and Haas Company, E. I. duPont de Nemours & Company, Gallowhur Chemical Corporation, Monsanto Chemical Company, Antara Chemicals, Niagara Chemical Company, Mallinckrodt Chemical Works, General Aniline and Film Corporation, Emulsion Corp., Colloidal Chemical Corp., Dow Chemical Company, Amchem Products, Inc., General Allied Chemical Corp., and others that may have been unintentially overlooked.

Martin and Gravatt (1954) described a physical method for saving white pines by excising all diseased bark tissue from trunk cankers and pruning off infected branches. To help prevent attacks from other fungi and from insects, bordeaux or an antiseptic paint was recommended for treating wounds of large cankers. This method of canker removal never proved practical in forestry because of high treatment costs and the technical skill required.

Cycloheximide history. Whiffen *et al.* (1946) first reported the production of the antifungal antibiotic, cycloheximide, by streptomycin-yielding cultures of *Streptomyces griseus.* Leach *et al.* (1947) isolated it in pure crystalline form and established its empirical formula in 1948 (Leach and Ford). Kornfeld *et al.* (1949) determined its chemical structure to be β—[2-(3,5-dimethyl-2-oxocyclohexyl)-2-hydroxyethyl]-glutarimide.

A literature survey covering the agricultural use of cycloheximide has been published (Ford *et al.* 1958). Cycloheximide was first applied commercially for turf disease control in 1952 and for cherry leaf spot, *Coccomyces hiemalis* Higgins, in 1954.

In forest disease control, Tarjan and Howard (1953) reported that foliar sprays of cycloheximide did not control Dutch elm disease, *Ceratocystis ulmi* (Schwarz) Buisman, on young trees. Strong and Klomparens (1955) found that a single application of 100 ppm cycloheximide to galls of *Gymnosporangium juniperivir ginianae* Schw. and *G. globosum* Farl. on eastern redcedar (*Juniperus virginiana* L.) prevented teliospore germination and sporidia production. By using a 0.5 percent summer oil spray mixture, effective control was obtained at 25 and 50 ppm cycloheximide. No foliage injury was observed. Caroselli (1957) reported that WK-34 gave good control of juniper blight, *Phomopsis juniperovora* Hahn, when applied to 1- or 2-year-old seedlings at the rate of 1 ounce of proprietary material per 10 gallons of aqueous solution. The spray solution contained 12 ppm cycloheximide and 675 ppm pentachloronitrobenzone. Phelps *et al.* (1957) reported that cycloheximide and its acetate delayed sympton expressions of oak wilt, *Ceratocystis fagacearum* (Bretz) Hunt, in over half the trees observed for a 3-month period. Solutions of the two materials were applied by the chisel-cone method.

Maloy and Matthews (1960) found that cycloheximide at concentrations of 1, 5, and 25 ppm was phytotoxic when applied directly to strobili of slash pine, *Pinus elliottii* var. *elliotii* Engelm., for control of southern cone rust, *Cronartium strobilinum* (Arth.) Hedge. and Hahn. Sprayed on the basal 4 feet of some trees approximately 1 week before strobili began to emerge from the buds and on others about 3 weeks after pollination had occurred, 150 ppm cycloheximide in an oil solution was not effective as a systemic fungicide in preventing or arresting the pathogen.

Klomparens (1951) found that the wood-rotting fungi, *Poria monticola* Murr. (*P. microspora* Overh.), *Lentinus lepideus* Fr., *Fomes igniaruis* var. *laevigatus* fr., *Lenzites trabea* (Pers.) Fr., and *Schizophyllum commune* Fr., were completely inhibited for 48 hours when grown on a malt extract agar containing 2 ppm cycloheximide. The wood-staining fungi, *Ascosybe grovesii* Wells, *Ceratocystis* (Endoconidiophora) *moniliformis* (Hedge.) Moreau, *Hormiscium gelatinosum*, *Ceratocystis* (Ophiostroma) *adiposa* (Butl.) Moreau, were completely inhibited by 0.1 to 10 ppm cycloheximide, but *Cadophora brunnescens* Davids and *Curvularia geniculata* (Tracy and Earle) Boedijn. required 100 ppm cycloheximide for complete inhibition.

Moss[1] reported that aqueous solutions of 10 and 20 ppm cycloheximide applied to foliage of 15- and 20-year-old western white pine generally inhibited production of blister rust pyniospores and accelerated

[1] Annual Report, Blister Rust Control, Northern Region, Forest Service, U.S. Dept. Agric., 1951.

the flagging of infected branches. Also, proximal limits of cankers on flagged branches failed to produce aeciospores the following spring. Trunk infections were neither arrested nor killed from translocated cycloheximide. In these same tests, cycloheximide caused a heavy cast of 2- and 3-year-old needles, but did not injure leaders, shoots, or new leaves.

Moss[2] found that more branch infections were killed by foliar spray when cycloheximide was combined with 2,4,5-trichlorophenoxyacetic acid and a surfactant. Solutions of 10 and 20 ppm cycloheximide were prepared with 1,000 ppm 2,4,5-trichlorophenoxyacetic acid and 0.1 percent adjuvant. Adjuvants in aqueous solution that gave good results and negligible damage to foliage were summer oil emulsion, propylene glycol, Tween #20, and Multifilm L. Solutions with Triton X-45 were the most effective, but more injurious to shoots and foliage.

The discovery that cycloheximide had a therapeutic effect against white pine blister rust infection in the perimeter of excised trunk cankers on western white pine was reported in 1957 (Moss). In these tests pure crystalline cycloheximide dissolved in acetone and diluted in Sovaspray 100 isoparaffinic base oil was 83, 77, and 80 percent effective at concentrations of 150, 300, and 600 ppm, respectively.

Statements in this paper concerning therapeutic effects are based on stoppage of fungus fruiting and cessation or retrogression rather than on histological examination of infected tissues. Cessation of fungus activity and subsequent healing of cankered areas is frequently referred to as "canker kill" and is considered *prima facie* evidence that the causal fungus has been killed. Though a canker still persists after being "killed," in the sense here used, it is no longer pathologically functional and is only as harmful to the host tree as any other mechanical injury of comparable size, severity, and location.

Moss (1958) reported that when the solute was diluted in No. 1 fuel oil,[3] 150 ppm cycloheximide had a completely deactivating effect on blister rust infections. In contrast, aqueous 2 percent glycerol solution, 150 ppm cycloheximide, was 62 and 55 percent effective while 150 ppm cycloheximide diluted in Sovaspray 100 was 83 and 79 percent effective on reproduction and pole-size western white pine, respectively.

Moss *et al.* (1960) described the procedures followed in applying cycloheximide by the basal stem method, and reported that by using this method over 4 million western white pines were treated in the northern Rocky Mountain region in 1959. The labor cost was 0.52 man-days per acre, on which an average of 232 trees were treated.

Lemin *et al.* (1960) utilizing both bioassay measurements and paper chromatographic identification from needle, bark, and xylem samples collected ½, 1, 2, 4, 8, 16, 32, 64, and 128 days after treatment found that cycloheximide is absorbed by, persists in, and is translocated upward in western white pine. The tissue samples were collected from pole-size trees treated with 120 ppm cycloheximide by the basal stem method. The upward movement of cycloheximide was reported to be through the water-conducting elements since the antibiotic was detected in xylem both at and above the site of application, but not in cortical tissue above the treated area of the trunk.

Trace amounts of cycloheximide were found in upper needles to 8 days, upper xylem to 4 days, lower needles to 8 days, lower xylem to 16 days, and treated lower bark to 2 years. The lower bark sample

[2] Serial Report No. 150, Fungicidal and phytotoxic properties of chemicals applied as foliage spray to western white pine infected with blister rust. Northern Region, Forest Service, U.S. Dept. Agric., Feb. 24, 1953.

[3] A volatile distillate oil for use in burners preparing fuel for burning solely by vaporization. It is marketed as stove oil in the Pacific Northwest and northern Rocky Mountain states.

was collected from a tree treated with 200 ppm cycloheximide. None was detected in untreated upper bark from trees treated with 120 ppm or 200 ppm cycloheximide. The assay solution had to contain 2.0 micrograms per cc to permit detection of measurable amounts of cycloheximide in tissue extractions.

Phytoactin history. Ziffer *et al.* (1957) reported the isolation of the polypeptide antibiotic phytoactin from fermentation whole cultures of an undescribed species of *Streptomyces.* It was effective against certain fungi and gram-positive bacteria. In greenhouse tests,[4] tomato late blight, *Phytophthora infestans* (Montagne) DeBary, was controlled with 93 ppm; and bean rust, *Uromyces phaseoli typica* (Pers) Wint., with 14 ppm phytoactin.

Sprague (1958) reported the control of powdery mildew, *Podosphaera leucotricha* (E. and E.) Salm., on potted pear seedlings with 2 sprayings of 100 ppm phytoactin applied 12 days apart. Dickens and Henderson (1959) stated that phytoactin showed promise in the control of powdery mildew of apples, giving 74.5 percent control at 200 ppm. Vaartaja (1959) reported that *in vitro* tests indicated phytoactin had value to conifers for the control of the damping-off fungi, *Rhizoctonia solani* Kuhn (*Pellicularia* praticola (Kotila) Flentje), and *Pythium debaryanum* Hesse.

Phytoactin was reported as effective for the control of powdery mildew of rose, zinnia, bean, cucumber, and squash; against the rusts of snapdragon and wheat; apple scab, *Venturia inaequalis* (Cooke) Winter, and for the experimental control of oak wilt, *Ceratocystis fagacearum* (Bretz) Hunt.[5] Also, it was effective against such common fungi as *Ascochyta, Botrytis, Cercospora, Helminthosporium, Sclerotina, Septoria,* and *Stemphylium.*

[4] Phytoactin and Phytostreptin brochure, Pabst Laboratories, Milwakee, Wis., Nov. 1957.

[5] Letter of Feb. 22, 1960 from Jack Ziffer, Head, Department of Microbiology, Pabst Laboratories, Milwaukee, Wis.

Screening Tests

Since 1949, the literature has been searched for new compounds worthy of testing for the control of white pine blister rust on western white pine. The proprietary materials selected are listed in two groups. Compounds in group I were studied in 1949 through 1953. Group II, the antibiotics, were tested during the years 1949 through 1959.

Group I compounds. Sodium pentachlorophenate; sodium trichlorophenate; zinc ethylene bisdithiocarbamate; zinc dimethyl bisdithiocarbamate; dinitro-o-cycle-hexylphenol; copper 8-quinolinolate; 8-hydroxyquinoline benzoate; dichloro diphenyl thiophene; p-cyclohexyl-2, 6-dinitrophenol; disodium ethylene bisdithiocarbamate; calcium sulfamate; isopropyl-N-(3-chlorophynyl) carbamate; rosin amine d-pentachlorophenate; polyvinylpyrolidone; alkyl aryl pyridinium chloride; phenyl mercurous monoethanol ammonium acetate; 2,4,5-trichlorophenol zinc salt; 2,5-dichlorophenoxyacetic acid; 3,4-dichlorophenoxyacetic acid; 2,4,5-trichlorophenoxyacetic acid; 2,4,6-trichlorophenoxyacetic acid; 2,4,5-trichlorophenoxypropionic acid; alpha-naphthaleneacetic acid.

Group II compounds. Actinomycin; Agrimycin; Albemycin; Amphotericin; Anisomycin; Bacitracin; Canicidin; Circulin; Clavacin; Chlortetracycline; Cycloheximide and its oxime, acetate, semicarbazone, thiosemicarbazone, acetoacetate, and methylhydrazone; Duramycin Endomycin; Filipin; Fradicin; Fungichromin; Gramacidin; Griseofulvin; Helixin; Hortesin; Ilotycin; Mycostatin; Mycothricin; Neomycin; Oligomycin; Patulin; Phytoactin; Phytostreptin; Pleocidin; Polycycline; Polymixin; Rimocidin; Streptomycin; Subtilin; Trichothecin; Tyrothricin; and Viomycin.

Candicidin (Ark and Alcorn, 1956) had been reported effective against the uredial stage of white pine blister rust on ribes, giving 98.2 and 93.1 percent control at the rate of 1:5,000 sprayed 2 and 24 hours

TABLE 1. Host and canker reaction to antibiotics in foliar spray tests on 15-year-old western white pine infected with blister rust.

Antibiotic and year applied	Concentration	Host reaction class[1]				Number cankers treated and percent killed					
						Branch type		Trunk type		Total	
		I	II	III	IV	Number treated	Percent killed	Number treated	Percent killed	Number treated	Percent killed
Cycloheximide (Acti-dione BR) 1957	50		X			7	86	11	54	18	67
	100		X			6	83	10	60	16	69
	150		X	X		9	100	11	73	19	85
	200		X	X		7	100	12	67	19	79
	Check	X				8	0	10	0	18	0
Cycloheximide oxime 1957	50		X			9	89	10	60	19	79
	100		X			6	100	12	67	18	72
	150		X	X		8	100	11	64	19	79
	200		X	X		8	100	10	60	18	78
	Check	X				6	0	11	0	17	0
Cycloheximide acetate 1957	50		X			7	71	11	55	18	61
	100		X			7	86	10	40	17	59
	150		X	X		9	89	10	50	19	68
	200		X	X	X	8	87	12	42	20	60
	Check	X				8	0	10	0	18	0
Cycloheximide semicarbazone 1957	50		X			8	87	10	60	18	72
	100		X			5	100	13	77	18	83
	150		X			9	100	11	73	20	85
	200		X	X		7	100	12	75	19	84
	Check	X				9	0	10	0	19	0
Phytoactin 1958	100	X				7	100	11	55	18	72
	200	X				8	100	14	71	22	82
	400	X				6	100	11	82	17	89
	800	X				9	100	10	80	19	89
	Check	X				8	0	11	0	19	0

[1] I, no injury; II, 2- and 3-year-old needles cast; III, current growth of branch shoots on lower crown injured or killed; IV, leader and lateral shoots of upper crown injured or killed.

before inoculation, respectively.

Chemicals were tested both by foliar spray and trunk canker slit methods. Foliar spray was applied with a mist-type compressed air sprayer held at a distance of 3 to 4 feet from trees to allow the solution to drift over foliage, forming droplets on the needles but not visibly wetting trunk and branch bark. In the slit method, the bark was cut at the four angular apexes of discoloration to assist spray penetration, then solution was sprayed over the surface of trunk cankers. Ten 15-year-old western white pines were treated with each compound concentration tested by the foliar spray and trunk canker slit methods.

Group I compounds were compared at concentrations of 500, 1000, 2000, and 4000 ppm. Aqueous solutions were prepared with 0.1 percent Tween #20 surfactant. Antibiotics were first applied at concentrations of 5, 10, 20, 40, and 80 ppm. When this proved too low a level, it was made standard procedure to test antibiotics at concentrations of 50, 100, and 200 ppm. Occasionally a manufacturer advised higher levels, in which case the antibiotic was tested at concentrations of 100, 200, 400, and 800 ppm.

To determine both host and pathogen reaction, chemicals were applied in June when western pine was in active growth and most susceptible to chemical injury. Trees and infections were examined late the same season and twice the following year. Blister rust infections were observed for color brilliancy, pycniospore and aeciospore production, parasitism by the purple

mold fungus, *Tuberculina maxima* Rostrup, cortical tissue necrosis, and growth of callus tissue.

Among the 66 chemicals screened by the foliar spray method, 2 were found to kill blister rust infections on western white pine. These were the antibiotics cycloheximide and phytoactin from species of *Streptomyces*. Both were apparently absorbed by foliage and were translocated to kill branch and trunk infections (Table 1). Cycloheximide and its oxime, acetate and semicarbazone caused the 2- and 3-year-old needles to drop. Shoots of lower branches were injured or killed by 150 ppm cycloheximide and its oxime and acetate and 200 ppm semicarbazone while 200 ppm acetate injured or killed leaders and branch shoots of upper crown growth. Biological action was highest from semicarbazone and lowest from acetate. Results from semicarbazone and phytoactin were comparable, but semicarbazone was phytotoxic at all concentrations.

In applying aqueous solution directly to trunk infections by the slit method, both cycloheximide and phytaoctin killed blister rust infections in cortical tissue of western white pine (Table 2). Cycloheximide was more effective than its derivatives or phytoactin in these tests. No side effects from the antibiotics were observed from this method of treatment.

TABLE 2. Canker reaction to antibiotics applied by the slit method to trunk cankers on 15-year-old western white pine.

Antibiotic and year tested	Concentration ppm	Trunk cankers: Number treated	Trunk cankers: Percent killed
Acti-dione BR	50	10	90
(Cycloheximide)	100	10	100
1956	200	11	100
	Untreated	10	0
Cycloheximide	50	11	70
oxime	100	10	90
1957	200	10	90
	Untreated	10	0
Cycloheximide	50	10	50
aacetate	100	10	80
1957	200	10	80
	Untreated	10	0
Cycloheximide	50	10	80
semicarbazone	100	11	91
1957	200	10	100
	Untreated	10	0
Phytoactin	50	10	80
1958	100	12	91
	200	10	90
	Untreated	10	0

Cycloheximide Tests

Basal stem method. The objective was to develop a practical method for year-round use on western pine which would kill all blister rust infections in a tree regardless of their developmental stage. Spray solution was applied to the lower portion of trunks and to about 18 inches of the proximal ends of branches of the treated bole. Trees over 12 feet tall were sprayed to a height of 5 feet. Spray was applied to the lower third of the trunk in trees less than 12 feet tall. All bark was visibly saturated with solution by spraying from two or more sides of a tree. The nozzle of the compressed air sprayer was held 12 to 18 inches from a tree to simultaneously wet both trunk and the proximal ends of branches.

Trees of good color and growth with less than two-thirds of the trunk circumference girdled by a canker were selected for testing. Insofar as possible, all canker stages were represented both on and above the treated trunk area so that branch and trunk infections would include juvenile, pycnial, and aecial stage cankers. All tests by the basal stem method were made with Acti-dione BR[6] diluted in No. I stove oil.

The first series of tests was made to establish lethal dosage rates of Acti-dione for the age classes of western white pine: 11 to 20, 21 to 40, and 41 to 60. In 1959, the 61- to 80-year-old and mature age classes were added to this study. Individual treatments were applied to 20 infected trees

[6] The Upjohn Company, Kalamazoo, Michigan, trademark of 4 percent w/w cycloheximide concentrate for white pine blister rust.

in each age class and replicated in the three periods, May-June, July-August, and September-October.

A second test compared two low-cost oil diluents, stove oil and Stoddard's solvent, separately and in four combinations as carriers for Acti-dione. Acti-dione, 50, 100, and 200 ppm, was applied in the July-August period to the two age classes of western white pine 11 to 20 and 21 to 40.

A third test determined whether or not a surfactant would, by lowering surface tension of the spray solution, increase bark penetration. The three surfactants, 0.1 percent, compared in this test were the Tritons: X-45, X-100, and X-155. Acti-dione, 50, 100, and 200 ppm, diluted in stove oil was applied in May-June and July-August periods to 15-year-old western white pines. This age was selected because young trees with thin bark are more apt to be injured by treatment, and the trunk infections have less bark surface broken by blister rust spore production.

A fourth test measured perimetrical diffusion of cycloheximide and its translocation from the treated trunk outward into branches. The perimetrical movement of the antibiotic was tested by applying spray solution to one side of the trunk opposite the blister rust canker. Outward translocation into branches was tested by applying a solution with a paintbrush to the bark surface of trunks only. Both tests were made on 20-year-old trees.

In these tests, a progressive type of biological action of the antibiotic was expressed in the effect on a blister rust canker. The yellowish-orange cortical tissue that outlined a canker margin first began to turn light brown. Progressively, the color darkened until all diseased tissue appeared blackish-brown. Then as new healthy growth developed, causing dead bark to crack around the canker margin, the blackish-colored tissue became shriveled and depressed, thus outlining the region of cortical tissue that was killed. The time it took the diseased area to turn black, shrivel, and appear depressed varied from a few months for small trees to about 18 months for pole-size and larger trees. One or 2 years after treatment, the dead bark around the canker margin starts to rise as callus tissue begins to grow over the canker wound.

Table 3 shows the results of testing the four cycloheximide concentrations (50, 100, 150, and 200 ppm) on the three age classes of western white pine (11-20, 21-40, 41-60) in the May-June, July-August, and September-October periods. Trunk and branch cankers of all developmental stages on and above the treated trunk area are combined in this table.

Cycloheximide, 50 and 100 ppm, was less effective on the younger than the older ages of western white pine. One contributing factor is the difference in bark characteristics and the greater spray volume required on the older trees to bring bark surface to the point of visible saturation. Volumes up to five times greater were required on the rough scaly bark surface of older trees. Another factor is the evaporation rate of spray. In the summer heat of July and August, spray solution evaporated 2 to 3 times faster from smooth bark surface of younger trees than from the crevices of scaly bark of older trees. In the 11- to 20-year-old class, cycloheximide, 50 and 100 ppm, was more effective on aecial and pycnial than on juvenile cankers located on the treated trunk area. This may be the result of better spray penetration where the smooth bark surface has been broken by spore production.

Cycloheximide, 150 and 200 ppm, killed both the trunk and branch infections throughout the tree in all age classes in this test. One trunk canker was measured at a height of 40 feet above ground level. The observation that cycloheximide is translocated upward in quantities sufficient to kill the pathogen above the treated trunk area was substantiated by paper chromatography and bioassay of extractions from needles, bark, and xylem samples (Lemin *et al.* 1960). Failure to kill some trunk cankers on the treated area was attributed

to an impermeable coating of pitch over the bark surface. These were subsequently killed by slitting the canker margin to allow spray penetration.

While cycloheximide treatments were effective in all growth periods, interesting observations were made in the time and manner of canker death. Infections on trees treated in July and later often did not die until after new growth was produced in May-June of the next year. It was fairly common to find aeciospores being produced in the spring before these cankers died during summer and fall months. Infections at the base and above the treated trunk area on trees sprayed in May-June usually died and callus tissue began to develop around the cankered area the same season (Fig. 1).

Stove oil alone was responsible for killing a few infections on the treated trunk area of trees. These were old infections characterized by large areas of dead cortical tissue that results from the girdling action of the organism in sporulating several years. Growth of the organism was confined to one or two small sections of the canker margin of these already weak infections. In this type of canker, stove oil penetration was aided by the porous bark surface of the infected trunk area. Applying the oil to juvenile and pycnial infections had no observed biological effect.

On untreated trees, a few branch cankers were killed naturally through girdling of the branch by the organism. This natural "flagging" (death of the branch beyond the canker) of an occasional infected branch usually is not very conspicuous unless branch infections are extremely numerous. Even then, only a small number of all the branches infected on a tree flag each year. In contrast, on treated trees all infected branches that have been girdled by the organism flag in the growing season following treatment. This phenomenon must result from cycloheximide killing mycelium that has transported assimilates for branch growth. Lachmund and Hansbrough (1934), studying truncated cankers

TABLE 3. Trunk and branch cankers killed with Acti-dione BR (cycloheximide) in stove oil applied by the basal stem method in the May-June, July-August, and September-October growth periods to 3 age classes of western white pine infected with blister rust.

Age class,[1] years	Cycloheximide (ppm)	Plant growth-period: May-June		July-August		September-October		Total	
		Cankers treated	Percent killed	Cankers treated	Percent killed	Cankers treated	Percent killed	Cankers treated	Percent killed
11-20	50	53	75	43	67	38	84	134	75
	100	47	85	51	73	46	91	144	83
	150	61	97	48	94	53	100	162	97
	200	55	95	46	96	51	98	152	96
	Oil	46	7	44	9	55	5	145	7
	Untreated	43	0	54	0	44	2	141	1
21-40	50	46	78	53	74	46	82	145	78
	100	59	83	49	78	51	92	159	84
	150	54	96	61	91	49	98	164	95
	200	48	100	55	93	56	96	159	96
	Oil	51	10	57	7	43	12	151	9
	Untreated	45	4	44	2	37	0	126	3
41-60	50	34	81	28	79	29	86	91	82
	100	29	86	37	84	24	92	90	87
	150	33	100	31	94	33	97	97	97
	200	30	97	27	96	28	100	85	99
	Oil	28	14	25	12	24	12	77	13
	Untreated	27	1	23	0	26	1	76	1

FIGURE 1. *Outline of blister rust canker on trunk in which fungus growth has been checked with cycloheximide (Acti-dione) on western white pine. Note cracking (arrow) of canker margin as callus tissue develops.*

to determine the period blister rust mycelium could continue to live and grow after all source of food supply had been cut off beyond the point of infection, found that the mycelium apparently stimulated a reversal of the flow of assimilates in the infected branch. Branch stubs of truncated cankers remained alive for periods ranging up to 5 years, whereas the branch stubs of checks all died within 1 year from the date of cutting.

Table 4 presents the results of testing three cycloheximide concentrations diluted in a mixture composed of different proportions of stove oil and Stoddard's solvent. Treatments in July and August were made on two age classes of western white pine: 11- to 20- and 21- to 40-year-old trees. Both of these diluents are low-cost carriers; they differ in volatility. As an example, Stoddard's solvent evaporated from bark surface about ten times faster than stove oil in temperatures above 90° F. Solvent was added to stove oil hoping it might increase bark penetration in periods of summer heat.

In these tests all concentrations of cycloheximide showed the best results when

TABLE 4. Canker reaction to cycloheximide in stove oil and Stoddard's solvent applied by the basal stem method to two age classes of western white pine in the July-August period.

	Diluent proportions		Cycloheximide concentration					
			50 ppm		100 ppm		200 ppm	
Age class, years	Stove oil, parts	Stoddard's solvent, parts	Cankers treated	Percent killed	Cankers treated	Percent killed	Cankers treated	Percent killed
11–20	1	0	17	82	12	92	19	100
	7	1	20	85	14	93	20	100
	3	1	16	81	14	86	15	100
	1	1	14	77	18	83	16	87
	0	1	17	65	13	69	21	81
	Untreated		19	0	16	0	18	0
21–40	1	0	15	93	16	100	14	100
	7	1	11	100	14	100	17	100
	3	1	13	100	16	94	10	100
	1	1	17	88	15	93	12	92
	0	1	19	79	12	67	14	79
	Untreated		15	0	17	0	13	0

TABLE 5. Canker reaction to cycloheximide in stove oil diluent with and without adjuvants,[1] applied to basal stems of 15-year-old western white pine in the May-June and July-August growth periods.

Growth period	Cycloheximide ppm	Stove oil[2]		Triton X-45		Triton X-100		Triton X-155	
		Cankers treated	Percent killed	Cankers treated	Percent killed	Cankers treated	Percent killed	Cankers treated	Percent killed
May-June									
	50	17	76	22	59	26	69	32	78
	100	24	87	19	74	32	78	36	83
	200	20	100	26	85	37	89	29	97
	oil	23	9	24	4	30	6	31	6
	Untreated	25	0	17	0	24	0	28	0
July-August									
	50	29	72	21	62	28	71	34	68
	100	33	85	27	70	35	83	30	80
	200	24	96	31	81	19	89	27	93
	oil	22	5	20	5	25	4	37	8
	Untreated	26	0	23	4	30	0	29	0

[1] Surface active agent 0.1 percent Triton X-45, Triton X-100, or Triton X-155.
[2] No surfactant added.

diluted in stove oil containing not more than 25 percent solvent. Canker kill decreased when a higher proportion of that solvent was used. This demonstrates the advantage in using a low-volatile diluent such as stove oil to increase time for absorption in summer heat. Stove oil also lasts longer as a marker to distinguish treated from untreated trees. At a temperature above 90°F, the bark surface was visibly wet with stove oil for 20 to 30 minutes, but solvent evaporated in 2 to 3 minutes. Below 90°F, bark surface sprayed with stove oil was visibly wet for periods ranging from 1 to 5 hours, whereas, Stoddard's solvent still evaporated in a matter of minutes.

Table 5 shows the results of using adjuvants to lower surface tension of stove oil and increase penetration of spray solution applied to the basal portion of trunks. Three cycloheximide concentrations and 3 surfactants (0.1 percent) were compared in treating 15-year-old western white pines in the May-June and July-August periods. Inclement weather and freezing temperatures prevented tests in September and October.

In the May-June period, the trunk bark of some of the younger trees was scalded by oil solution containing a surfactant. This necrosis extending to xylem occurred in patches, which were more predominant on south than north trunk exposures. Oil solution with Triton X-45 was the most injurious; Triton X-155 was least harmful to the bark surface of trunks. All injury to bark surfaces was observed to occur when trees were actively growing in May and June. As the season advanced, trees became increasingly tolerant to oil spray containing a surfactant.

In the July and August period, the trunk bark of young trees was injured only by spray solution containing Triton X-45. The older and larger trees were not affected by this spray solution applied in the July-August period. There was no appreciable difference between cycloheximide concentrations in the amount of injury in either period. Also, there was no indication that these surfactants in oil solution increased the effectiveness of low cycloheximide concentrations in treating trees of young age classes.

In the test to measure perimetrical diffusion of cycloheximide by applying spray solution to the side of the trunk opposite the blister rust canker, no trunk or branch infections on the unsprayed side of the trunk

were killed. All infection both on and above the treated area of the sprayed side of the trunk were killed. This suggests that the upward translocation of cycloheximide is in vascular alignment with the treated area of the trunk.

In a test to measure outward translocation into branches by applying a spray solution with a paintbrush to the bark surface of trunks only, cycloheximide killed 27 percent of the branch infections on the treated trunk area as against 100 percent when 12 to 18 inches of the proximal ends of branches were also sprayed. Where spray solution was applied only to the bark surface of trunks, approximately 90 percent of the branch infections alive 1 year later occurred on the lower half of the treated trunk area. With either way of applying solution, all infections above the treated trunk area were killed. This suggests that the quantity of cycloheximide translocated outward into branches increases from the base to the top of a 20-year-old western white pine tree.

Foliar spray treatment. Cycloheximide and its oxime and semicarbazone, 100, 200, and 400 ppm, diluted in aqueous solution and in 10 percent and 20 percent oil emulsion were tested in 1958 for possible subsequent trials by aircraft application. Triton B-1956 (0.1 percent) was added to the aqueous solution as a wetting agent. Triton X-155 was used to emulsify stove oil and water. Spray solution was applied with a compressed air backpack sprayer at a distance of 3 to 4 feet from a tree to allow solution to drift over foliage without visibly wetting trunk and branch bark. In the selection of 15 trees for each treatment, an effort was made to obtain as many as possible with both trunk and branch infections.

The results of these tests are presented in Table 6. Treatment effects on branch infections are not included because all were killed by foliar spray. Biological effects on trunk cankers were noted as follows: (1) The number killed generally increased slightly with the percentage of oil used in

TABLE 6. Canker reaction to cycloheximide aqueous and oil emulsion foliar sprays applied to 15-year-old western white pine in the May-June and July-August growth periods.

Growth period	Cycloheximide		Diluents					
			Aqueous		Oil emulsion 10 pct.		Oil emulsion, 20 pct.	
	Form	Concentration ppm	Cankers treated	Percent killed	Cankers treated	Percent killed	Cankers treated	Percent killed
May-June	Acti-dione BR (Cycloheximide)	100	17	59	24	67	16	75
		200	21	71	20	70	18	78
		400	23	78	18	83	25	84
		Diluent	19	0	15	0	18	0
		Untreated	15	0	15	0	21	0
May-June	Cycloheximide oxime	100	18	56	25	69	24	71
		200	15	64	21	67	20	70
		400	23	74	17	76	21	81
		Diluent	19	0	24	0	19	0
		Untreated	17	0	24	0	22	0
May-June	Cycloheximide semicarbazone	100	26	69	16	75	18	79
		200	21	76	20	75	21	81
		400	24	79	18	83	19	89
		Diluent	18	0	22	0	23	0
		Untreated	23	0	27	0	20	0
July-August	Cycloheximide semicarbazone	100	25	64	17	71	17	74
		200	19	68	20	75	26	77
		400	21	71	23	78	22	81
		Diluent	20	0	18	0	23	0
		Untreated	18	0	15	0	25	0

the spray solution. (2) Only semicarbazone was translocated downward in sufficient quantity to kill trunk cankers below the lowest live branches. (3) Semicarbazone effect was less in the July-August period.

Cycloheximide and its derivatives proved toxic; the minimum injury was from semicarbazone. Length of leader growth in 1959 on trees sprayed with cycloheximide and its oxime, 400 ppm, was reduced about one-third of normal. Injury to foliage ranged from casting of 2- and 3-year-old needles with 100 and 200 ppm to killing shoots of lower branches with 400 ppm. Leader and branch shoots in the upper crown were not deformed or killed. This suggests that shoot injury of the lower crown is due to a slower evaporation rate of solution from the lower sheltered branches than from the upper exposed branches of a tree.

In 1959, cycloheximide (LC-657), 100 ppm, and its semicarbazone, 100, 200, and 400 ppm, in 20 percent oil emulsion were applied by helicopter to a 25-year-old western white pine stand. Spray volume applied was 10 gallons per acre to plots 10 acres in size. Plots were sprayed on June 2 and 3. In each plot, 100 trees were paint marked and permanently tagged to observe host and pathogen reactions. The 100 trees selected for treatment observation were carefully chosen for vigor and the most active infections, excluding any with cankers in advance stages of girdling trunks.

Marked trees in these plots were examined in May 1960 and again in August to obtain preliminary results of the aerial spray treatments. Final observations will be made in 1961 to allow 2 years for biological action. By August 1960 all damaging branch cankers (those within 18 inches of the bole) had been killed. The percentage of trunk cankers killed ranged from 60 to 80 percent. Semicarbazone, 200 ppm, had killed the greatest number of trunk cankers. Cycloheximide (LC-657), 100 ppm, and semicarbazone, 400 ppm, results are comparable and fall about midway between semicarbazone 100 and 200 ppm. The only visible injury from the aerial application of cycloheximide and its semicarbazone was casting of 2- and 3-year-old needles in a 3-week period following spraying.

In late May 1960, and again in mid-September, additional tests in aerial spraying were made in 41- to 60- and 21-40-year-old western white pine stands. In May, cycloheximide semicarbazone, 200 ppm, thiosemicarbazone, 200 ppm, and methylhydrazone, 100, 200, and 400 ppm, in 20 percent oil emulsion were applied by helicopter at 10 gallons per acre to 10-acre plots. In mid-September, two 100-acre plots were sprayed by helicopter with 7 gallons of solution per acre consisting of semicarbazone and methylhydrazone in 20 percent oil emulsion. Two small acreage plots were sprayed with special formulations of semicorbazone and one with methylhydrazone. In addition, a 450-acre plot was sprayed with semicarbazone, 7 gallons of solution per acre, by fixed-wing plane. Final results of the aerial spray tests will be reported in a later paper.

Soil drench treatment. Root absorption of antibiotics as a means of immunizing nursery-grown western white pine seedlings from blister rust infection to permit the early outplanting of controlled burns was explored.

In 1958, cycloheximide and its oxime, acetate, and semicarbazone, 25, 50, 100, and 200 ppm, were applied by pouring 200 ml aqueous solution on the soil surface of each 7-inch pot of 1- and 3-year-old trees. Twenty seedlings were treated in each instance. These were potted 5 weeks, and the solution applied 2 weeks before the seedlings were artificially inoculated.

The inoculation procedure used a polyethylene-covered frame enclosure and an overhead sprinkler system installed 4 feet high in aisles between beds to maintain optimum moisture-temperature conditions for infection. For inoculum, branches of telia-bearing ribes leaves were heeled upright in the seedling pine pots The expos-

ure period was 80 hours. Seedlings were re-inoculated in 1959 and 1960.

In 1959, cycloheximide thiosemicarbazone, 25, 50, 75, and 100 ppm, was included in further testing oxime and semicarbazone on 1-, 2-, and 3-year-old western white pine seedlings potted in May. Solution was applied 4 weeks before seedlings were artficially inoculated in October. A 14x16-foot tent was used in place of the polyethylene enclosure. In 1960, cycloheximide methylhydrazone was added to the 1959 series of tests. Except as noted, 1958 procedures were followed in subsequent tests.

In these soil drench tests, cycloheximide and its acetate and thiosemicarbazone proved more toxic than oxime, semicarbazone, and methylhydrazone to all seedling ages of western white pine. For example, the compounds that were highly phytotoxic to all seedling ages, thiosemicarbazone, 25, 50, 75, and 100 ppm, killed 19, 52, 73, and 84 perecnt respectively.

One-year-old seedlings were more susceptible to chemical injury than 2-year-old seedlings, and these in turn were more susceptible than 3-year-old seedlings. Three-year-old seedling mortality from thiosemicarbazone, 25, 50, 75, and 100 ppm, was 0, 29, 75, and 100 percent, respectively.

The cycloheximide derivatives, oxime, semicarbazone, and methylhydrazone, had little or no effect on the western white pine seedlings. No injury resulted from oxime and methylhydrazone nor from semicarbazone except in the treatment of 1-year-old seedlings where 100 ppm killed a maximum of 20 percent. No seedling mortality occurred with 25 ppm semicarbazone.

Seedling immunization from blister rust infection varied between cycloheximide derivatives and the concentrations applied to soil. Antibiotic effects in preventing infection were noted as follows: (1) The most effective compound in preventing infection was a low concentration of thiosemicarbazone, followed by oxime, semicarbazone, acetate, and cycloheximide. Results of methylhydrazone treatments in 1960 are not available for this paper. Thiosemicarbazone, 25 ppm, gave complete protection without injury to 3-year-old seedlings exposed to a single artificial inoculation from blister rust. (2) The percentage of seedlings infected increased as the antibiotic concentration increased. To illustrate, seedling infection for trees treated by oxime, 25, 50, 75, and 100 ppm, was 14, 16, 30, and 22 percent, respectively. Untreated seedlings were 44 percent infected from a single artificial inoculation.

Slurry root-dip treatment. Dipping seedling roots in a slurry prior to outplanting is another possible antibiotic treatment to immunize western white pine from blister rust infection. Powder forms of cycloheximide oxime, acetate, semicarbazone, and methylhydrazone, 0.4, 0.2, 0.1, 0.05, and 0.025 percent, were mixed with twice their weight in water for slurry concentrations of 0.133, 0.067, 0.0335, 0.0167, and 0.0083 percent, respectively. With about 60 g of formulated mud sticking to the roots, seedlings were treated with amounts equivalent to 80, 40, 20, 10, and 5 mg of antibiotic, respectively. Cycloheximide powder at half these strengths was tested also.

Seedlings were lifted from a transplant bed, their roots submerged in the slurry, and immediately replanted in the nursery on September 3, 1959. Twenty 2-1 seedlings were used to test each antibiotic concentration. They were watered by overhead sprinklers until mid-October rain. The loss of foliage from treatment prevented seedlings from being artificially inoculated. All had died by June 1960.

Phytoactin Tests

This polypeptide antibiotic, as well as cycloheximide, is being tested for the treatment of western white pine by basal stem, foliar spray, soil drench, and slurry root-dip methods. Tests to develop application techniques for phytoactin began in 1958 while cycloheximide studies started in 1949.

Basal stem tests in 1959 employed phytoactin, 100, 200, and 400 ppm, diluted in isopropanol co-solvent before adding stove

oil to the mixture. These solutions were applied to the basal portion of the trunks of 15-year-old trees. In foliar spray tests, phytoactin, 100, 200, and 400 ppm, aqueous solutions were applied by helicopter to sapling, pole, and mature stands of western white pine. A single plot in a cutover area naturally regenerating to western white pine was also sprayed with phytoactin, 200 ppm. Procedures in establishing and spraying 10-acre plots with phytoactin were identical including dates of treatment, June 2 and 3. In foliar spray tests on white bark (*Pinus albicaulis* Engelm.) and limber (*P. flexilis* James) pines in Glacier National Park, phytoactin was applied with a backpack compressed air sprayer.

In 1960, foliar spray plots were established both in May and in September. The spring plots were sprayed by helicopter and airplane; fall plots were sprayed only by helicopter. Sizes of plots sprayed in May by helicopter and airplane were 20 and 80 acres, respectively. Size of plot sprayed in the fall by helicopter was 100 acres. The age classes of western white pine sprayed in May and September were 41 to 60 and 21 to 40 years, respectively.

In May, phytoactin (L-318), 200 ppm, aqueous solution and 10 percent and 20 percent oil emulsions were compared at volume rates of 5 and 10 gallons spray per acre. In addition, four 20-acre plots were sprayed with water soluble (L-382 and L-387) and oil emulsion (L-390 and L-395) forms of phytoaction, 200 ppm, applied at the rate of 10 gallons spray per acre. In September, the equivalent amount of phytoactin (L-318 and L-395) per acre was applied in a volume of 7 gallons spray per acre to two 100-acre plots.

Phytoactin, 100, 200, and 400 ppm, soil drench treatments began in 1959. Procedures used 1-, 2-, and 3-year-old western white pine seedlings that were potted, treated, and artificially inoculated by methods similar to those described for testing cycloheximide and its derivatives. Tests in the slurry root-dip treatment of seedlings began in 1960. Except for dosage rates, 4, 2, 1, 0.5, and 0.25 percent, procedures in seedling treatment were the same for both phytoactin and cycloheximide derivatives. Plantings were made in the nursery and in the field. In the field, seedlings were planted in association with ribes in a controlled-burn area. Ten percent of these outplanted tree seedlings were artificially inoculated in October 1960.

Phytoactin applied by the basal stem method was about as effective as equivalent concentrations of Acti-dione on, but not above, the treated trunk area of western white pine. In this test phytoactin killed less than half of all blister rust infections above the treated trunk area. The percent of infections killed above the treated trunk area increased as the concentration of phytoactin increased. This suggests that with the 100 to 400 ppm concentrations the amount of phytoactin translocated upward was not sufficient to kill all blister rust infections above the treated trunk area.

Preliminary examination of plots sprayed by helicopter in 1959 shows better results from phytoactin in aqueous solution than from cycloheximide (LC-657) and its semicarbazone in 20 percent oil emulsion. Preliminary results further indicate that both antibiotics are more effective at 200 than at 100 or 400 ppm. Phytoactin was not injurious to foliage of any age, whereas cycloheximide (LC-657) and its semicarbazone caused sprayed western white pines to cast all their 2- and 3-year-old needles. There were no harmful side effects on the associated species. Final results of this study will become available late in 1961.

In soil drench tests so far concluded phytoactin has had some harmful side effects on both seedling roots and mycorrhizae. Root and mycorrhizae damage has varied from conditions of discoloration to some seedling roots being necrotic. Root and mycorrhizae damage generally increased with dosage rate of phytoactin applied to seedlings. At the time of writing, the above-ground parts of seedlings are of normal color and growth. The full impact of

root and mycorrhizae damage will not be known until later.

Phytoactin in solution containing the surfactant Triton X-155 protected seedlings exposed to a single artificial inoculation from blister rust. Its effectiveness as a soil drench increased with the amount of surfactant in solution. For example, after 2-year-old trees were treated with phytoactin, 100 ppm, aqueous solution containing 0.025, 0.05, and 0.1 percent Triton X-155, seedling infection from a single artificial inoculation was 30, 11, and 0 percent, respectively. Untreated trees were 44 percent infected. By recent observation, the results of treatment in seedling protection from blister rust infection are about the same for phytoactin, 100, 200, and 400 ppm, concentrations and for 1-, 2-, and 3-year-old seedlings.

Treating 2-1 western white pine seedlings by the slurry root-dip method resulted in high mortality (90 to 95 percent) in the nursery. Treated seedlings outplanted in a control-burned area had 68, 52, 33, 28, and 26 percent mortality for phytoactin dosage rates of 4, 2, 1, 0.5, and 0.25 percent, respectively. Seedling mortality of the control was 18 percent. The difference in mortality rates between treated seedlings planted in the nursery and in the field suggests that artificial watering in the nursery was responsible for more rapid dissolution and root uptake of phytoactin than occurred in the field.

Summary

Sixty-six compounds were screened by *in vivo* testing to discover a chemotherapeutant and/or prophylactic to control blister rust on western white pine. Two antifungal antibiotics from the genus *Streptomyces* were found to have systemic action when applied to and absorbed by foliage, roots, and trunk bark of trees.

Acti-dione (cycloheximide) biological action on blister rust infections was first observed from foliar spray tests on western white pine in 1949. An effective treatment known as the excise method for saving trees from blister rust was developed in 1953. In this method, dead and dying bark was removed from trunk cankers and resultant wounds sprayed with Acti-dione isoparaffinic oil solution. Branch infections were destroyed by pruning. Then in 1956 the slit method was developed. It was accepted for control work in 1957. These two methods differ in the way trunk cankers were prepared for spray treatment. In the slit method, bark was incised at the four angular apexes of canker margin discoloration to aid spray penetration. Both methods required tree examination for infections, surgery to expose mycelium to antibiotic solution, and pruning off diseased branches.

A more practical and economical treatment known as the basal stem method was developed in 1957. It eliminated the technical and costly tasks of tree examination and tree surgery required in the excise and slit methods. In the basal stem method, the basal portion of trunks and proximal ends of attached branches of trees of good color and growth are sprayed with 150 ppm cycloheximide diluted in No. 1 fuel (stove) oil. Trees over 12 feet tall are sprayed to a height of 5 feet while trees less than 12 feet tall have only the lower third of the trunk sprayed. All bark surface is visibly drenched with solution.

Cycloheximide was lethal to all canker stages on and above the treated trunk area on trees less than 60 years old in these tests. Both trunk and branch infections to a height of 40 feet in pole-size trees were killed with cycloheximide by the basal stem method. The observation that cycloheximide was translocated upward in the trunk in quantities sufficient to kill the fungus above the treated trunk area was substantiated by paper chromatography and bioassay analyses of extractions from needle, bark, and xylem samples. The upward movement of cycloheximide apparently was through the water-conducting elements.

The basal stem method was effective in May through October, but infections on trees treated in the July-August and Sep-

tember-October periods often were not killed until after new growth was produced in May-June of the next year. In this case, biological action was delayed until active growth the next spring. Aecial cankers on trees sprayed in the July-August and September-October periods occasionally fruited the following spring unless cankers were directly sprayed. From 12 to 18 months were usually required to kill infections on trees sprayed during these two periods. Infections on and above the treated trunk area on trees sprayed in the May-June period usually were killed and callus tissue began to develop the same season.

Cycloheximide results were affected by the volatility of the diluent. Best results were obtained with stove oil (No. 1 fuel oil) or a dilution containing not less than 75 percent stove oil. A low volatile diluent increased absorption time and served a useful purpose as a marker to distinguish treated from untreated trees. In contrast, Stoddard's solvent evaporated from the bark surface about ten times faster than stove oil in temperature above 90°F.

Trunks of small trees were injured by cycloheximide stove oil solution when adjuvants were added to lower surface tension to increase absorption. In contrast, cycloheximide stove oil solution was not injurious except when applied to exposed trunks of open growing trees less than 20 years old in the May-June period. Thereafter, young trees showed increasing tolerance to stove oil as the season advanced.

Cycloheximide and its oxime, acetate, and semicarbazone in aqueous solution applied with backpack sprayer to the foliage of western white pine were effective on branch infections but killed only 56 to 79 percent of the trunk infections. In a comparison of aqueous solutions and oil emulsions, antibiotic effect on trunk cankers increased when oil in the emulsion was increased from 10 to 20 percent. Cycloheximide and its derivatives were about equally effective in these tests. All caused trees to cast 2- and 3-year-old needles.

Cycloheximide and its semicarbazone in 20 percent oil emulsion and phytoactin in aqueous solution were applied from helicopter in 1959. All damaging branch infections (cankers within 18 inches of the bole) were killed. The percentage of trunk infections killed within 1 year ranges from 60 to 80 percent. Phytoactin has been more effective in these tests than cycloheximide and its semicarbazone. Both antibiotics have been more effective at 200 than 100 or 400 ppm. Final results will be compiled later, allowing 2 years for biological action after treatment.

In May and again in September 1960, phytoactin and cycloheximide were applied from both helicopter and fixed-wing aircraft. Purposes of these tests were to further evaluate soluble and emulsion forms of the antibiotics and compare diluents and types of aircraft used to apply spray.

Soil drench and slurry root-dip methods of antibiotic treatment to immunize nursery-grown western white pine seedlings from blister rust infection were investigated. Phytoactin in solution containing a surfactian, 0.1 percent, was promising as a protectant but had some harmful side effects on seedling roots and mycorrhizae. The full impact of root and mycorrhizae damage to seedlings is not yet known. Cycloheximide and its derivatives, except methylhydrazone, appear to be too toxic to seedlings for a practical nursery soil drench treatment.

In the nursery under artificial watering, the antibiotics killed 90 percent or more of the seedlings treated by the slurry root-dip method. Seedlings outplanted in a control burn area had mortality rates of 26 to 68 percent at concentrations of 0.25 and 4 percent phytoactin, respectively.

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INDEX TO VOLUME 7, FOREST SCIENCE, 1961

Art.—article; rev.—review; art. (rev.)—review of article or book by.

Authors are indicated by capitals.

Abies. Colchicine—induced polyploidy in. art. 314
Air-layering of lodgepole pine and origin of adventitious roots. art. 227
ALLARD, R. W. rev. 336
ALLEN, ROBERT M. art. 342
ANDERSON, ROGER F. rev. 129
Antibiotics for control of blister rust on western white pine. art. 380
ARNEMAN, H. F. art. 160
ASHBY, WILLIAM CLARK. art. 273
Aspen, quaking. Influence of gibberellic acid on growth and fiber length of. The. art. 43
Aspen stands, Minnesota. Organic layers in, and their role in soil improvement. art. 66
ATKINS, M. D. art. 197
Baker, F. S. art. (rev.) 370
BAKER, W. L. art. (rev) 351
BARNES, ROBERT L. art. 130
Basswood, American. Responses of Seedlings to several light intensities. art. 273
Beetle, Douglas-fir. Intraspecific competition as a factor in the control of. art. 197
Bending strength of California red fir. The effect of site and other factors on specific gravity. art. 106
Blister rust on western pine. Antibiotics for control of. art. 380
Bormann, F. H. art. 247
BOWDEN, ALVIN B. art. 147
BRINKMAN, KENNETH A. art. 35
BRÜNING, DETLOV. rev. 23
BRYAN, W. C. art. 123
Bubenik, Antonin. rev. 173
Buds, adventitious. Air-layering of lodgepole pine and origin of adventitious buds. art. 227
CAROLIN, JR., V. M. art. (rev.) 129
CARVELL, K. L. art. 98
Colchicine—induced polyploidy in *Abies*. art. 314
Computer technique for the study of forest sampling methods. A. art. 282
Cone initiation in southern pines. Stem elongation and time of. art. 149
Conifers, The. rev. 294
COOPER, CHARLES F. art. 72
Counter, dot. An electric. art. 146
CROW, A. B. art. 373
Crown competition—a measure of density art. 35
Culture, synthetic, of mycorrhizae of southern pines. art. 123
CUNNINGHAM, T. M. rev. 370
Cycloheximide on growth of mycorrhizal fungi and mycorrhizae of pine. Influence on. art. 376
CZARNOWSKI, M. S. rev. 281
DANA, SAMUEL TRASK, RUSSELL N. CUNNINGHAM, and JOHN H. ALLISON. 372
DANIELS, JOE M. art. 2
DAUBENMIRE, R. art. 24
DAVIDSON, ROSS W. art. (rev.) 368
DDT in a forest soil. The persistence of. art. 194
DECKER, JOHN P. art. 218
Defects. Detecting in by the attenuation of gamma rays. art. 136
DELLA-BIANCA, LINO. art. 320
Density, crown competition—a measure of. 35
Detecting defects in wood by the attenuation of gamma rays. art. 136
Discharges, peak. Reduction in associated with reforestation. art. 232
Distribution of some true firs of the Pacific coast. New data on. art. 349
Douglas-fir seed, maturation of. A biochemical study. art. 204
DOUGLASS, JAMES E. art. 265
Drainage effects on slash pine and loblolly pine seedlings. Flooding and. art. 2
Dry-matter content of loblolly pine needles appears unrelated to geographic seed source. art. 373
DUFFIELD, JOHN W. art. (rev.) 319
Dynamics of even-aged forest stands. 281
ECHOLS, R. M. art. 147, 369
EGGLER, WILLIS A. art. 149
EIBERLE, KURT. rev. 26
EINSPAHR, DEAN W. art. 43
Electric dot counter. An. art. 146

Environmental factors on the abundance of oak regeneration beneath mature oak stands. The effect of. art. 98
Equations for the description of past growth in even-aged stands of ponderosa pine. art. 72
Equations used in constructing volume tables. Index for comparing. art. 337
Eucalyptus regnans. The natural regeneration of. art. (rev.) 370
FERGUS, CHARLES L. rev. 368
Fertilization, forest. rev. 23
Fiber length of quaking aspen. The influence of gibberellic acid on growth and. art. 43
Field identification of roots of conifers in the Inland Empire. art. 352
Fir, California red. The effect of site and bending strength on specific gravity of. art. 106
Firs of the Pacific coast. New data on distribution of some true. art. 347
FLEMMICH, C. O. rev. 379
Flooding and drainage effects on slash pine and loblolly pine seedlings 2
Foliar absorption and translocation of phosphorus by loblolly pine seedlings. art. 330
Forest and shade tree entomology. rev. 129
Forest needs lime. The. rev. 175
Forestry Theses Accepted by Colleges and Universities in the United States, Supplement July 1959-June 1960. art. 295
Forstdüngung. rev. 23
Foundations of wildlife nutrition. rev. 173
FOWELLS, H. A. art. (rev.) 256
FURNIVAL, GEORGE M. art. 337
GATHERUM, GORDON E. art. 144
GAUSSEN, H. rev. 176
Geographic seed source. Dry-matter content of loblolly pine needles appears unrelated to. art. 373
Gibberellic acid, the influence of. On growth and fiber length of quaking aspen. art. 43
GILBERTSON, R. L. art. 352
GINGRICH, SAMUEL F. art. 35
GREEN, R. LAMAR. art. 2
Growth and survival of the oak wilt fungus in oak blocks. art. 306
Growth in even-aged stands of ponderosa pine. Equations for the description of past. art. 72
Growth, jack pine. Some forest soil characteristics and their relationship to. art. 160
Growth, seedling, of eastern hemlock. Effects of photoperiod and source on. art. 81
HACSKAYLO, EDWARD. art. 376
HADDOCK, PHILIP G. art. 349
Hardwoods, southern. Rot entrance through dead branches of. art. 218
HASEL, AUSTIN A. art. (rev.) 281
Hemlock, eastern. Effects of photoperiod and source on seedling growth of. art. 81
HEWLETT, JOHN D. art. 265
Hila of full and empty longleaf pine seeds distinguishable. art. 246
HORWITZ, LEAH G. art. 52
Identification, field, of roots of conifers in the Inland Empire. art. 352
Illustrated genera of wood decay fungi. rev. 368
Index for comparing equations used in constructing volume tables. An. art. 337
Intraspecific competition as a factor in the natural control of the Douglas-fir bettle. art. 197
JOHNSON, F. D. 352
KENADY, REID. art. 146
KOZLOWSKI, THEODORE T. art. 177, 357
KRAJICEK, JOHN E. art. 35
KRAMER, PAUL J. art. 342
KRUSSMANN, BERD. rev. 294
KUKACHKA, B. FRANCIS. art. rev. 379
Laurel, mountain. Seasonal variation in the moisture content of the green leaves of. art. 16
LEAF, ALBERT L. art. (rev.) 23
LEAPHART, C. D. art. 352
LESTER, DONALD T. art. 314
Light intensity under forest canopies. Variation in measurements of. art. 144
Light intensities. Responses of American basswood seedlings to several. art. 273
Liquid dispersion method for mounting wood fibers on slides. art. 369
LITTLE, JR., ELBERT L. art. (rev.) 176, 294
Loblolly pine. rev. 158
Maturation of Douglas-fir seed—a biochemical study. art. 204
MERGEN, FRANCOIS. art. 314
Method for calculating error of soil moisture volumes in gravimetric sampling. A. art. 265

McDERMID, W. rev. 256
McGREGOR, WM. H. DAVIS. art. 342
McLEMORE, B. F. art. 246, 373
McMULLEN, L. H. art. 197
Minnesota lands. rev. 372
Moisture content of the green leaves of mountain laurel. Seasonal variation in the. art. 16
MOSS, VIRGIL D. 380
Mounting wood fibers on slides. Liquid dispersion method for. art. 369
Movement of water in trees. The. art. 177
Mycorrhizae of pine. Influence of cycloheximide on growth of mycorrhizal fungi and on. art. 376
Mycorrhizae of southern pines. Synthetic culture of. art. 123
Natural regeneration of *Eucalyptus regnans*. The. art. (rev.) 370
NAYLOR, AUBREY W. art. 130
NIENSTAEDT, HANS. art. 81
Oak regeneration beneath mature oak stands. The effect of environmental factors on. art. 98
Oak wilt fungus in oak blocks. Growth and survival of the. art. 306
OLSON, DAVID F. JR. art. 320
OLSON, J. S. art. 81
O'REGAN, W. G. art. 282
Organic layers in Minnesota aspen stands and their role in soil improvement. art. 66
Ornithine, radioactive. Utilization of by germinating embryos of longleaf and slash pines. art. 130
OSBORN, KATHERINE H. art. 295
PALLEY, MARSHALL N. art. 52, 282
PARRISH, WAYNE B. art. 136
PARTRIDGE, ARTHUR D. art. 306
PAULEY, SCOTT S. art. 116
PAWLUK, STEVE. art. 160
Persistence of DDT in a forest soil. The. art. 194
Photoperiod and source on seedling growth of eastern hemlock. Effects of. art. 81
Photoperiod. The effect of on growth, photosynthesis, and respiration of loblolly pine seedlings from two geographic sources. art. 342
Piedmont hardwood and pine-hardwood upland forests. Soil-site studies in. art. 320
Pine, eastern white, stumps. Intraspecific root-grafting and the survival of. art. 247
Pine, jack. Growth. Some forest soil characteristics and their relationship to. art. 160
Pine, lodgepole. Air layering of and origin of adventitious buds. art. 227
Pine, loblolly, seedlings. Foliar absorption and translocation of phosphorus by. art. 330
Pine, loblolly, seedlings from two geograpic sources. The effect of photoperiod on growth, photosynthesis, and respiration of. art. 342
Pine, ponderosa. Equations for the description of past growth in even-aged stands of. art. 72
Pine, ponderosa. Vegetative indicators of rate of height growth in. art. 24
Pine, slash, and loblolly pine seedlings. Flooding and drainage effects on. art. 2
Pine, western white. Antibiotics for control of blister rust on. art. 380
Point sampling estimators. Properties of some random and systematic. art. 52
Polyploidy in *Abies*. Cochicine-induced. art. 314
Principles of plant breeding. art. (rev.) 336
Properties of some random and systematic point sampling estimators. art. 52
Provenance and progeny tests in tree improvement programs. Some considerations on the statistical design for. art. 116
Rays, gamma. Detecting defects in wood by attenuation of. art. 136
REDISKE, J. H. art. 204
Reduction in peak discharges associated with reforestation. art. 232
REIFSNYDER, WILLIAM E. art. 16
Responses of American basswood seedlings to several light intensities. art. 273
Ring analyzer, inexpensive. For cumulative summerwood measurements. art. 147
Root grafting, intraspecific, and the survival of eastern white pine stumps. art. 247
Roots of conifers in the Inland Empire. Field identification of. art. 352
Rot entrance through dead branches of southern hardwoods. art. 218
Salt secretion by *Tamarix pentantra*. Pall. art. 214
Sampling, gravimetric. A method for calculating error of soil moisture volumes in. art. 265
Sampling methods, forest. A computer technique for the study of. art. 282
Sampling, systematic point. Properties of some random estimators and. art. 52
SCHNEIDER, WILLIAM J. art. 232
SCHNIEWIND, ARNO P. art. 106

SCHOPMEYER, C. S. art. 330
SCHULTZ, VINCENT. rev. 319
Seasonal variation in the moisture content of the green leaves of mountain laurel. art. 16
Seed—a biochemical study. Maturation of Douglas-fir. art. 204
Seeds, longleaf pine, distinguishable. Hila of full and empty are. art. 246
SHIUE, CHERNG-JIANN. art. 116
Shoot elongation characteristics of forest trees. art. 357
Site and other factors on specific gravity and bending strength of California red fir. The effect of. art. 106
Soil characteristics and their relationship to jack pine growth. Some forest. art. 160
Soil fertility in a Douglas-fir—red alder plantation. Stand development and. art. 238
Soil improvement. Organic layers in Minnesota aspen stands and their role in. art. 66
Soil moisture volumes in gravimetric sampling. A method for calculating error of. art. 265
Soil-site studies in Piedmont hardwood and pine-hardwood upland forests. art. 320
Solar radiation, total. Variations in three Norway spruce plantations. art. 257
Specific gravity and bending strength of California red fir. The effect of site and other factors on. art. 106
SQUILLACE, A. E. art. (rev.) 336
STAHELIN, R. art. (rev.) 145, 264
Stand development and soil fertility in a Douglas-fir—red alder plantation. art. 238
Statistical design for provenance and progeny tests in tree improvement programs. Some considerations on the. art. 116
Statistics in ecology—a search of periodicals. An annotated bibliography on the uses of. art. (rev.) 319
Stem elongation and time of cone initiation in southern pines. art. 149
STOECKELER, JOSEPH H. art. 66
Structure and increment of beech stands. The. rev. 264
Stumps. Intraspecific root-grafting and the survival of eastern white pine. art. 247
Symposium on forest types and forest ecosystems. rev. 145
TABER, RICHARD D. art. (rev.) 173
Tamarix pentantra. Pall. Salt secretion by. art. 214
TARRANT, ROBERT F. art. 238
Taxonomic monograph on pines. rev. 176
Tests in tree improvement programs. Some considerations on the statistical design for provenance and progeny. art. 116
Timber utilization in Malaya. rev. 379
THATCHER, T. O. rev. 351
TOOLE, E. RICHARD. art. 218
Translocation of phosphorus by loblolly pine seedlings. Foliar absorption and. art. 330
TRYON, E. H. art. 98
Utilization of radioactive ornithine by germinating embryos of longleaf and slash pines. art. 130
Use of chemicals in southern forests. The. rev. 256
VAN BUIJTENEN, J. P. art. 43
Variation in measurements of light intensity under forest canopies. art. 144
Variations in total solar radiation in three Norway spruce plantations. art. 257
Vegetative indicators of rate of height growth in ponderosa pine. art. 24
VÉZINA, P. E. art. 257
Volume tables. An index for comparing equations used in constructing. art. 337
WAHLENBERG, W. G. rev. 159
WAKELEY, P. C. art. (rev.) 158, art. 373
WALKER, LAURENCE C. art. 2, art. (rev.) 175
WARD, RICHARD C. art. 357
Water in trees. The movement of. art. 177
WEST, WILLIAM I. art. 295
Wilt, oak. Fungus in oak blocks. Growth and survival of the. art. 306
WOODWELL, GEORGE M. art. 194
YIM, KYONG BIN. art. 227
YODER, RAY A. art. 295
ZAK, B. art. 123
ZASADA, Z. A. art. (rev.) 372

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Tables: Each table should be typewritten on a separate sheet, given a title at the top, and should be numbered consecutively. Footnotes used in tables should be designated by numerals.

Illustrations and Figures: An illustration—whether a photograph, a line drawing, a map, or a graph—is designated as a figure. A caption, typewritten on a separate sheet, should be submitted for each illustration.

All figures should be numbered consecutively. On the margin or back of each illustration should be written lightly in soft pencil the number of the figure, the name of the author, and an abbreviated title.

Photographs should be printed on glossy paper, and should not be smaller than 4 by 5 inches. Illustrations larger than 8½ by 11 inches ordinarily are not acceptable. Authors may indicate by sketches the manner in which they wish the components of complex illustrations to be laid out. The *Style Manual for Biological Journals* offers good suggestions regarding legibility, size, and labelling of illustrations. All line drawings and lettering should be in India ink. High standards of neatness in drafting and lettering of illustartions will be observed. Lettering should be sufficiently large to withstand drastic reduction and still be legible.

Footnotes: To indicate a footnote, place a superior figure after the word that refers to the note. Consecutive numerals should be used, never asterisks.

Use footnotes to give credit to unpublished material and communications. If only a few references to literature are made (less than one per 1000 words), complete literature citations may be given in footnotes rather than in a separate listing.

Literature Cited: Designate references to literature citations by the author's name and year of publication inserted in parentheses at the appropriate place in the text. If there are more than two authors, list only the senior author's name in the text with the abbreviation *et al.* Example: (Smith *et al.* 1954). Only published references should be given in *Literature Cited*. Periodical abbreviations should follow *Guide to the use of Forestry Abstracts*, Commonwealth Forestry Bureau, Oxford, England, 1950.

Nomenclature and Terminology: When a species is first mentioned in a paper, its common name must be immediately followed by its italicized scientific name, with authority abbreviation, in parentheses. The authority for nomenclature of North American tree species is *Check List of Native and Naturalized Trees of the United States*, Agriculture Handbook 41, Forest Service, U. S. Dept. Agric. Washington, D. C., 1953. Authorities for nomenclature of other plants and of animals are listed in the *Style Manual for Biological Journals*. Technical usage in forestry and allied fields follows *Forestry Terminology*, 3rd Edition, Society of American Foresters, Washington 6, D. C. 1958.